1 w
8810

PROCEEDINGS

OF THE

California Academy of Sciences

Volume 45

SAN FRANCISCO
PUBLISHED BY THE ACADEMY
1987–1988

PUBLICATIONS COMMITTEE

Tomio Iwamoto, *Scientific Editor*

Mary Christine Cunningham, *Managing Editor*

Luis F. Baptista

Thomas F. Daniel

Daphne G. Fautin

Thomas Moritz

Wojciech J. Pulawski

(US ISSN 0068-547X)

The California Academy of Sciences
Golden Gate Park
San Francisco, California 94118

PRINTED IN THE UNITED STATES OF AMERICA
BY ALLEN PRESS, INC., LAWRENCE, KANSAS

CONTENTS OF VOLUME 45

		Pages
No. 1.	FAUTIN, DAPHNE GAIL. *Stylobates loisetteae,* a new species of shell-forming sea anemone (Coelenterata: Actiniidae) from Western Australia. Published August 19, 1987	1–7
No. 2.	ROSS, EDWARD S. Studies in the insect order Embiidina: A revision of the family Clothodidae. Published September 10, 1987	9–34
No. 3.	IWAMOTO, TOMIO, AND YU. I. SAZONOV. A review of the southeastern Pacific *Coryphaenoides* (sensu lato) (Pisces, Gadiformes, Macrouridae). Published February 5, 1988	35–82
No. 4.	BRIGGS, THOMAS S., AND KEVIN HOM. A new species and new records of schizomids from the central coastal California (Schizomida: Schizomidae: *Schizomus*). Published February 5, 1988.	83–88
No. 5.	ANDERSON, M. ERIC. *Eucryphycus,* a new genus of California eelpout (Teleostei: Zoarcidae) based on *Maynea californica* Starks and Mann, 1911. Published February 5, 1988	89–96
No. 6.	GOEDERT, JAMES L. A new Late Eocene species of Plotopteridae (Aves: Pelecaniformes) from northwestern Oregon. Published February 5, 1988	97–102
No. 7.	ROSENBLATT, RICHARD H., AND JOHN E. MCCOSKER. A new species of *Acanthemblemaria* from Malpelo Island, with a key to the Pacific members of the genus (Pisces: Chaenopsidae). Published February 5, 1988	103–110
No. 8.	DANIEL, THOMAS F. A systematic study of *Bravaisia* DC. (Acanthaceae). Published February 5, 1988	111–132
No. 9.	LAWS, RICHARD A. Diatoms (Bacillariophyceae) from surface sediments in the San Francisco Bay estuary. Published February 5, 1988	133–254
No. 10.	MILLER, WILLIAM, III, AND SAMUEL D. MORRISON. Marginal marine Pleistocene fossils from near mouth of Mad River, northern California. Published April 12, 1988	255–266
No. 11.	ANDERSON, M. ERIC. Studies on the Zoarcidae (Teleostei: Perciformes) of the southern hemisphere. II. Two new genera and a new species from temperate South America. Published April 12, 1988	267–276
No. 12.	LANDRUM, LESLIE R. The myrtle family (Myrtaceae) in Chile. Published December 7, 1988	277–317
Index to Volume 45		319–329

The Scientific Publications Committee acknowledges with thanks the individuals listed below who served as manuscript reviewers for this volume.

John A. Barron, Gregor Cailliet, Daniel M. Cohen, James C. Cokendolpher, Joel L. Cracraft, L. H. Durkee, William N. Eschmeyer, Carter R. Gilbert, David Greenfield, Cadet Hand, Tomio Iwamoto, David H. Kavanaugh, Richard N. Mariscal, Lucinda McDade, Rogers McVaugh, Nigel Merrett, Ralph T. Montgomery, Wojciech J. Pulawski, Barry Roth, Rudolf Schmid, William Shear, Robert Stanton, David L. Stein, Kenneth I. Warheit.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 1, pp. 1–7, figs. 1–6 August 19, 1987

STYLOBATES LOISETTEAE, A NEW SPECIES OF SHELL-FORMING SEA ANEMONE (COELENTERATA: ACTINIIDAE) FROM WESTERN AUSTRALIA

By

Daphne Gail Fautin

Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

ABSTRACT: *Stylobates loisetteae* new species, the third species in this genus of deep-water, shell-forming sea anemones, is described. Occurring in seas off the northern coast of Western Australia, at depths of 300–500 m, this new species is symbiotic with a presumably undescribed hermit crab of the genus *Parapagurus*.

Received February 28, 1986. Accepted May 14, 1986.

INTRODUCTION

Certain species of sea anemones commonly attach to gastropod shells occupied by hermit crabs. As the crustacean grows, it is obliged to exchange its current shell for increasingly larger ones. At least two lineages of sea anemones have the ability to secrete extensions of such shells (carcinoecia) so that the crustaceans presumably need to change abodes less frequently or not at all. The acontiarian lineage includes the European cloak anemone, *Adamsia palliata,* and *Paracalliactis.* The only endomyarian shell-formers known belong in the genus *Stylobates* (family Actiniidae). These anemones can construct large trochoid carcinoecia, an important component of which is chitin (Dunn and Liberman 1983). Each of the two previously described species of this taxon is associated with a different species of *Parapagurus.* Knowledge of this unusual association was summarized by Dunn, Devaney, and Roth (1980).

I describe a third species of *Stylobates* that is symbiotic with an undescribed species of *Parapagurus.* These anemones, like others of the genus, occur only in deep water. The large size attained by their hermit crab associates may be possible at such depths only because their lives do not depend on a supply of sizable gastropod shells. Such shells may be rare in deep water not only because large organisms are less numerous than smaller ones but perhaps more importantly because calcium carbonate dissolves more easily with depth (Correns 1955). Thus, association with carcinoecium-forming actinians may have allowed large hermit crabs to live in an environment they could otherwise not have exploited.

MATERIALS AND METHODS

I examined 15 alcohol-preserved specimens of actinians and their associated carcinoecia and 5 additional carcinoecia no longer associated with the anemones that made them, all from seas off the northern coast of Western Australia.

Histological sections 8 μm thick were stained

with hematoxylin and eosin. Cnidae were measured from seven specimens, although not all tissues of each individual were examined. In the section "Size and distribution of cnidae," n represents the total number of capsules measured, and N is the ratio of the number of animals in which that type of cnida was found to the number examined. Ranges are given for length and width, with measurements for single capsules falling outside the normal range given in parentheses.

Type specimens have been deposited at the Western Australian Museum (WAM), Perth, Western Australia; the Australian Museum (AM), Sydney, New South Wales; and the California Academy of Sciences (CAS), San Francisco, California.

Description

Stylobates loisetteae new species

Base.—Completely adherent to carcinoecium; concave, conforming to its shape. Edge smooth but outline irregular due to curvature of shell. Covers entire shell except for small area at beginning of last whorl (Fig. 1b, 2). Thin, with mesenterial insertions visible as dark lines; color same as that of column.

Column.—Smooth, in preservation colorless to light pink or yellow, ectoderm frequently sloughed off. Diameter to 75 mm. Thin, with mesenterial insertions visible typically as dark lines (Fig. 1a), but insertions of lower orders may be marked in maroon. Occasionally torn, with mesenterial filaments protruding (Fig. 1a). Fosse shallow. Directive axis coincident with shell's axis of coiling. Nearly bilaterally symmetrical, with plane of symmetry perpendicular to directive axis; length on short side 15–30 mm in specimens studied, on long side 25–65 mm. Bulged at shell's apex (Fig. 1a, 2).

Endodermal sphincter (Fig. 3) well-developed, circumscribed, with mesogleal shaft (thick in most) from which arise pinnately arrayed lamellae that may tend to a reticulate pattern (Fig. 3a); ovoid (Fig. 3a) to deltoid (Fig. 3b) in cross-section. Presumably weak, to judge by expanded oral disc and exposed tentacles in all specimens examined.

Oral Disc and Tentacles.—Oral disc flat, to 55 mm diameter; color same as that of column. Round, central mouth typically agape in preserved specimens (Fig. 1a). Marginal tentacles

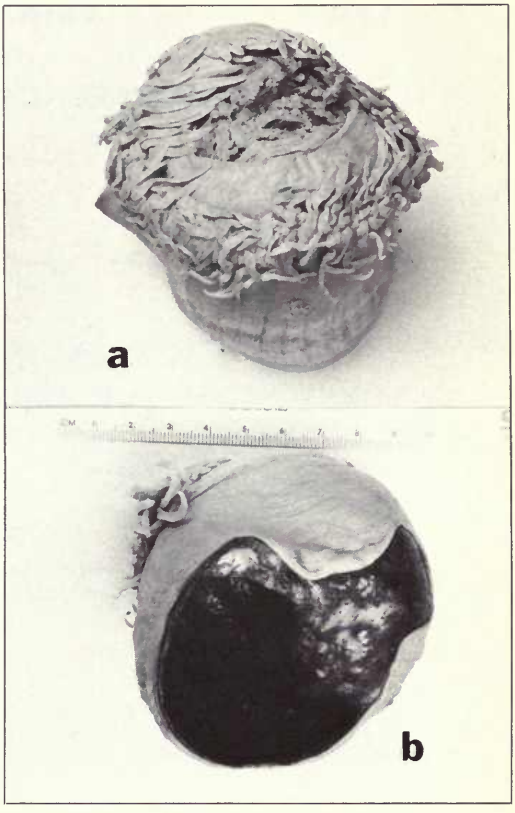


Figure 1. Paratype specimen of *Stylobates loisetteae* (WAM 21-84). Note that pedal disc envelops entire carcinoecium save for that portion at beginning of ultimate whorl.

thin, pointed (Fig. 1, 2); inner ones to 20 mm long, progressively shorter marginally; about 160 total counted in one medium-sized specimen, nearly 200 in a large one.

Ectodermal musculature longitudinal in tentacles, radial in oral disc.

Mesenteries and Internal Anatomy.—Mesenteries thin; no stomata seen. At least first two orders complete; five or six cycles in individuals of average size. Retractor muscles moderately well developed, diffuse (Fig. 4); occasional muscle bundles sunken into mesoglea. Parietobasilar muscles poorly developed. Mesenteries of two highest orders gametogenic; sexes presumably separate—only females seen. All developmental stages of ova may occur in a single mesentery; ova in section to 950 μm diameter.

Actinopharynx shallowly ribbed, with two symmetrical siphonoglyphs.

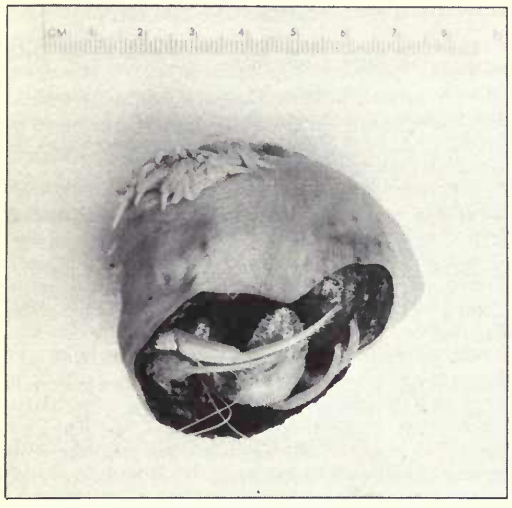


FIGURE 2. Paratype specimen of *Stylobates loisetteae* (AM G 15227).

CARCINOECIUM.—Varies from thin chitinous coating on large gastropod shell (Fig. 5), to massive trochoid carcinoecium (Fig. 1, 2) produced entirely by actinian except for minute apical snail shell. Maximum diameter of actinian-produced carcinoecium among material examined 85 mm with aperture 40 × 55 mm (WAM 18-84). Golden color and gloss, although alcohol-preserved specimens tend to dull and turn chalky when dried. Umbilicus shallow to absent.

CNIDOM.—Spirocysts, basitrichous isorhizas (basitrichs), microbasic *p*-mastigophores.

Size and distribution of cnidae (letters refer to components of Fig. 6).

Tentacles

spirocysts (a) 21.1–55.8 × 2.5–3.7 μm
n = 63 N = 6/6

basitrichs (b) 29.8–39.7 × 2.5–3.7 μm
n = 70 N = 6/6

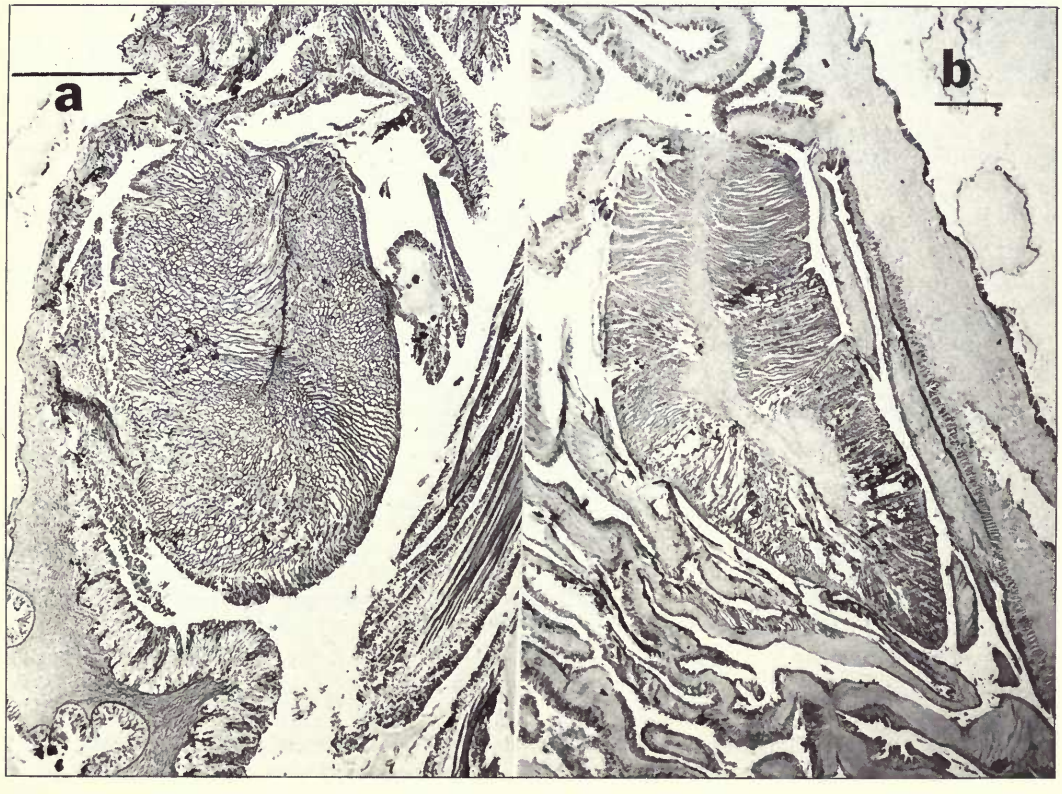


FIGURE 3. Cross-section of sphincter muscles of *Stylobates loisetteae* (a: paratype WAM 21-84; b: holotype WAM 18-84). Scale = 500 μm.

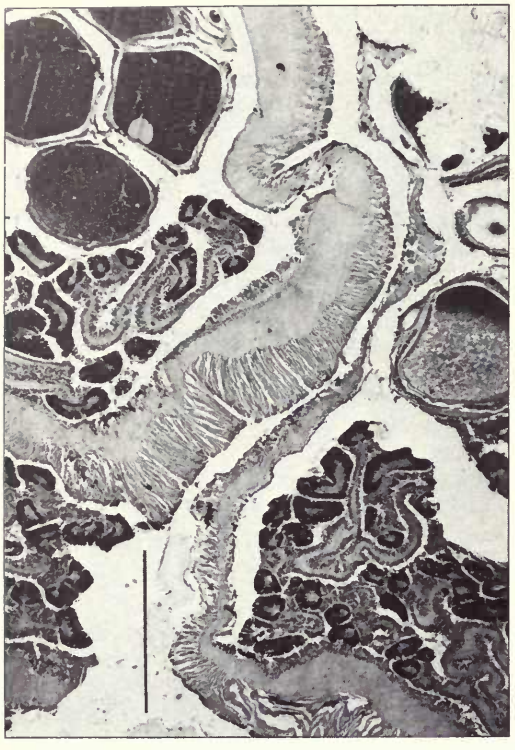


FIGURE 4. Cross-section through mesenteries of *Stylobates loisetteae* (holotype WAM 18-24). Note retractor muscles and ova. Scale = 1 mm.

basitrichs (c) 9.9–16.1 × 1.6–2.5(4.0) μm
n = 11 N = 3/6
Actinopharynx
basitrichs (d) 26.0–37.2 × 2.5–3.7 μm
n = 59 N = 5/5
Column
basitrichs (e) 21.1–33.5 × 2.5–3.7 μm
n = 46 N = 5/5
Mesenterial filaments
basitrichs (f) 28.5–37.2 × 4.7–6.0 μm
n = 34 N = 5/7
basitrichs (g) 28.5–37.2 × 2.5–3.5 μm
n = 11 N = 3/7
basitrichs (h) 12.4–16.1 × 1.9–3.1 μm
n = 10 N = 4/7
microbasic *p*-mastigophores (i)
23.6–32.2 × 3.5–6.2 μm n = 50 N = 7/7

With one exception in the seven specimens examined, an individual possesses either wide (f) or narrow (g) basitrichs in its mesenterial filaments.

Type Specimens and Locality

HOLOTYPE.—One female specimen on empty shell, WAM 18–84 (Fig. 3, 4), collected by Loisette M. Marsh at 18°41′S, 116° 45–47′E (station SO2/82/46, 145 nautical miles (269 km) NW of Port Hedland, Western Australia), at 506–508 m from a muddy bottom, on 13 April 1982; along with histological sections—five slides of the sphincter and five of mesenteries.

PARATYPES.—Two specimens, each on an empty shell, WAM 21–84 (Fig. 1, 3), collected by P. Berry and N. Sinclair at 18° 06′S, 118°10′E (station COR/83/04, SW of Imperieuse Reef, Rowley Shoals, Western Australia), at 353–356 m from a muddy bottom, on 17 August 1983; along with histological sections from one specimen—five slides of the sphincter and five of mesenteries.

One actinian and its carcinoecium (separated), WAM 177–83, collected by Loisette M. Marsh at 18°20′S, 118°00′E–18° 19′S, 118°01′E (station SO2/82/37, 124 nautical miles (230 km) NNW of Port Hedland, Western Australia), at 320 m, on 10 April 1982; along with histological sections—four slides of the sphincter and three of mesenteries.

Six actinians (four on shells containing hermit crabs, one on an empty shell, and one detached) plus a naked, empty shell, CAS 052762, collected by P. Berry and N. Sinclair at 18°06′S, 118°10′E (station COR/83/04, SW of Imperieuse Reef, Rowley Shoals, Western Australia), at 353–356 m from a muddy bottom, on 17 August 1983; along with histological sections from one specimen—six slides of the sphincter and five of mesenteries.

Five specimens, each on a shell, two of which are occupied, AM G 15227 (Fig. 2), collected by P. Berry and N. Sinclair at 18° 05′S, 118°10′E (station COR/83/02, SW of Imperieuse Reef, Rowley Shoals, Western Australia), at 400–401 m from a muddy bottom, on 17 August 1983; along with histological sections from one specimen—five slides of the sphincter and five of mesenteries.

Three dry shells (one with a thin chitinous coating, one with a thick chitinous coating and a half whorl extension, and a high-spired coated one with nearly a full whorl of trochoid chitinous extension) CAS 052763 (Fig. 5), collected by Loisette M. Marsh, NW of Port Hedland, Western Australia (precise locality unknown) in April 1982.

ETYMOLOGY.—*Stylobates loisetteae* honors Loisette M. Marsh, Curator in the Department of Marine Zoology of the Western Australian Museum, for her many contributions to the natural history of the eastern Indian Ocean, and for her admirable concern in sending specimens from the Western Australian Museum to interested scientists.

GEOGRAPHICAL DISTRIBUTION.—Twenty-nine specimens of this species have been collected under the auspices of the Western Australian Museum near Port Hedland and Imperieuse Reef—in the area 18–19° S and 117–118.5° E—at depths of 300–500 m. Bottoms where these animals were dredged are characterized as muddy.

Discussion

Differential Diagnosis

Comparisons with the other species of *Stylobates*—*S. aeneus* and *S. cancrisocia*—are based on data in Dunn, Devaney, and Roth (1980). Carcinoecia of *S. loisetteae* vary more than

those of *S. aeneus*. This may be related to the nature of the original gastropod shell, which in *S. aeneus* is always very small, so that the carcinoecium is almost entirely a production of the anemone. By contrast, a high proportion of the *S. loisetteae* specimens examined (and the only one of *S. cancrisocia*) occur on large shells, which the anemone coats with chitinous material. Extensions of these shells, although invariably trochoid regardless of the shell's morphology, are frequently of uneven diameter and thickness. Carcinoecia entirely produced by actinians of the new species, despite being thicker and firmer than those of the other two species, may be knobby and bumpy. Growth lines of *S. loisetteae* carcinoecia, whether entirely produced by the actinian or on a large gastropod shell, may be wavy, in contrast to their concentricity in *S. aeneus*. The carcinoecium of *S. aeneus* has a deep umbilicus, unlike that of *S. loisetteae*.

Orientation of the actinian on the carcinoecium differs as well. Looking down upon the three-part symbiotic unit as it would be in life with the hermit crab extended from the carcinoecium, the apex of the shell is on the crustacean's right side and the actinian's tentacle crown faces rearward (the orientation of the specimen in Figure 2 is precisely upside down of this). In *S. aeneus*, the tentacle crown is on the parapagurid's left side (fig. 1b in Dunn, Devaney, and Roth 1980). It appears from Carlgren's (1928, plate II, fig. 6–9) illustrations that the oral disc of *S. cancrisocia* occupies a position even nearer the carcinoecium's aperture than it does in *S. aeneus*, being almost directly beneath the mouth of the parapagurid. This orientation so resembles that of the hormathiid anemone *Adamsia palliata* with respect to its host, *Pagurus prideauxi*, that Carlgren (1928) named the genus *Isadamsia* (see Dunn, Devaney, and Roth 1980, for discussion of nomenclature).

Nematocysts also differentiate *Stylobates loisetteae* from the two previously described species, with allowance made for the data on *S. cancrisocia* cited by Dunn, Devaney, and Roth (1980) having been taken from a single individual. Spirocysts (Fig. 6a) are broader in both other species, particularly *S. aeneus*. Large tentacle basitrichs (Fig. 6b) are smaller in *S. cancrisocia*. Small tentacle basitrichs (Fig. 6c) were not found in either of the other species. Only *S. aeneus* is reported to possess small basitrichs in the actinopharynx.

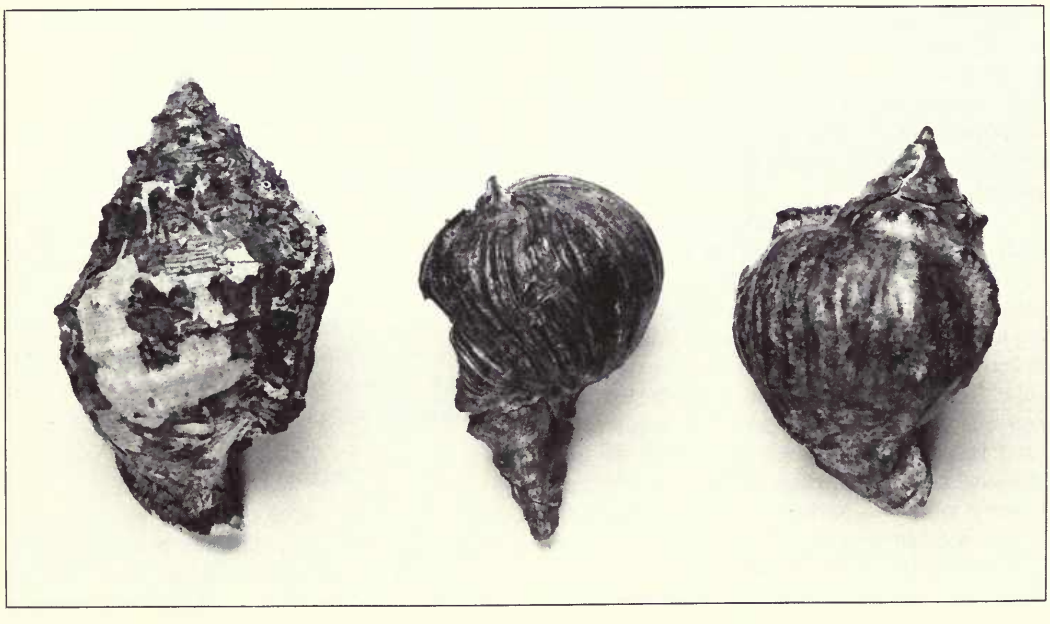


FIGURE 5. Three dry carcinoecia of *Stylobates loisetteae* (paratypes CAS 052763). That at left is a massive shell covered by a thin veneer of chitinous material. The coating on the right-hand specimen is thick and extends for half a whorl beyond the lip of the gastropod shell. The actinian extended the carcinoecium on the high-spired shell at center for nearly a full whorl; note that the actinian-produced portion is trochoid, regardless of the geometry of the founder gastropod shell.

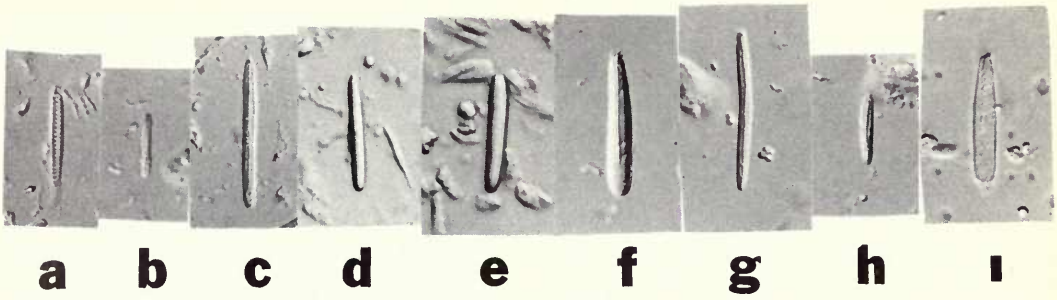


FIGURE 6. Cnidae of *Stylobates loisetteae*. Scale = 10 μm. Refer to text for explanation.

Column basitrichs (Fig. 6e) tend to be larger in *S. aeneus,* there being more overlap with *S. loisetteae* than with *S. cancrisocia.* The larger filament basitrichs are of similar length in all three species, but those of *S. cancrisocia* are broad (like Fig. 6f), whereas those of *S. aeneus* appear to be entirely of the narrow form (like Fig. 6g). The smaller filament basitrichs (Fig. 6h) tend to be larger in *S. aeneus.* Microbasic *p*-mastigophores of the filaments (Fig. 6i) are smaller in *S. cancrisocia.*

Natural History

The symbiont of *Stylobates loisetteae* is an as yet undescribed species of *Parapagurus* (Marsh pers. comm.). *Stylobates aeneus* is associated with *P. dofleini,* and *S. cancrisocia* with *P. trispinosus.* Thus there appears to be species specificity in this exclusively deep-water relationship. Moreover, the three known species of *Stylobates* are distributed allopatrically.

I have found the body wall of living specimens of *Stylobates aeneus* to be unusually thin and easily ruptured, in contrast to the typically thick, tough columns of deep-water actinians. The walking legs of *Parapagurus dofleini* are notably long; indeed, the word *stylobates* means "a walker on stilts" (Dunn, Devaney, and Roth 1980). Long legs allow the hermit to carry its carcinoecium (and associated anemone) well above the substratum, thereby making the delicate actinian, which is vital to its partner's continued existence, less vulnerable to injury. The situation in *S. cancrisocia* is unclear, and I have been unable to reexamine the one known specimen (see Dunn, Devaney, and Roth 1980), but the position of the anemone's oral disc, beneath the hermit's mouth, suggests that the hermit must hold the actinian aloft.

The initial portion of the ultimate whorl of the carcinoecium is exposed in every specimen of *Stylobates loisetteae* examined, and several bear evidence of that surface having been abraded or scuffed. This is perhaps unremarkable since it is the ventralmost portion of the shell, but it differs from *S. aeneus* (many tens of which I have examined, alive and preserved). I infer from this that the parapagurid carries its carcinoecium very low, or even drags it along the substratum, as hermit crabs commonly do. If the anemone were oriented on the carcinoecium as is *S. aeneus,* the oral disc would be scuffed against the substratum and the tentacles possibly snagged. I posit the rearward displacement of *S. loisetteae* to be an associated adaptation to raise the tentacle crown and thereby protect the thin-walled anemone.

Carlgren's (1949:60) definition of *Isadamsia* includes the sentence "The species of the genus live in symbiosis with hermit crabs in such a way that their mouths are always situated beneath that of the hermits (as in *Adamsia*)." However, he remarks (p. 95) that the various species of *Paracalliactis* differ in the positioning of their mouth relative to that of their hermit. Clearly the precise orientation of the anemone on the carcinoecium is not a feature of generic significance but is a specific coadaptation to a partner's habitus.

ACKNOWLEDGMENTS

Without the loan of specimens by Loisette M. Marsh, this study would have been impossible. Jim Patton, California Academy of Sciences photographer, took the macrophotos and cheerfully printed them and the photomicrographs. Barbara E. Weitbrecht contributed, as usual, her technical talents. Cadet Hand and Richard N. Mariscal provided useful editorial remarks.

Literature Cited

Carlgren, O. 1928. Actiniaria der Deutschen Tiefsee-Expedition. Wiss. Ergeb. Deutsch. Tiefsee-Exp. 22:123–266.

———. 1949. A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria. K. Svensk. Vetenskapsakad. Handl., ser. 4, 1(1):1–121.

Correns, C. W. 1955. Pelagic sediments of the North Atlantic Ocean. Pp. 373–395 *in* Recent marine sediments—a symposium, P. D. Trask, ed. Soc. Econ. Paleontol. Mineral. Spec. Publ. 4.

Dunn, D. F., D. M. Devaney, and B. Roth. 1980. *Stylobates*: a shell-forming sea anemone (Coelenterata, Anthozoa, Actiniidae). Pac. Sci. 34(4):379–388.

Dunn, D. F. and M. H. Liberman. 1983. Chitin in sea anemone shells. Science 221:157–159.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 2, pp. 9–34, 12 figs. September 10, 1987

STUDIES IN THE INSECT ORDER EMBIIDINA: A REVISION OF THE FAMILY CLOTHODIDAE

By

Edward S. Ross

Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

ABSTRACT: All thirteen species of Clothodidae are treated. The following taxa are new or recombined: *Clothoda longicauda* n. sp. (Peru); *Cryptoclothoda spinula* n. gen. and sp. (Brazil); *Antipaluria panamensis* n. sp. (Panama); *A. marginata* n. sp. (Colombia); *A. urichi* (Saussure), n. comb. (Trinidad); *A. intermedia* (Davis), n. comb. (Venezuela); *A. caribbeana* n. sp. (Venezuela); *A silvestris* n. sp. (Venezuela). *Chromatoclothoda* n. gen. (Amazon Basin); *C. elegantula* n. sp. (middle Amazon); *C. aurata* n. sp. (Peruvian montaña); *C. albicauda* n. sp. (Colombian montaña); *C. nigricauda* n. sp. (Peruvian montaña); *C. nana* n. sp. (Peruvian montaña).

Received June 23, 1986. Accepted September 19, 1986.

INTRODUCTION

In the South American family Clothodidae, especially in the genus *Clothoda,* the order's greatest concentration of plesiomorphic embiid features occurs, for example, almost perfect symmetry of male terminalia and the most complete, most uniformly cuticularized wing venation. If only the genus *Clothoda* were known, the family status would be unquestionable. However, I have recently discovered new species in the new genus *Chromatoclothoda*, and these species exhibit increasing specialization toward that of genera placed in other families.

Nevertheless, the family is retained as a natural group for genera in which males have symmetrical, unlobed cerci in combination with dentate mandibles, strongly cuticularized wing veins, anterior branch of media always forked, and little or no development of terminalia processes or lobes. Only in certain genera of the highly distinct Anisembiidae is there comparable symmetry of the cerci, but in these cases other portions of the terminalia are much more complex, wing venation is greatly reduced, and the mandibles lack multiple apical dentation.

Diversification of Clothodidae is of great evolutionary interest, for within the genus *Chromatoclothoda* are the beginnings of two major trends in terminalia structure and the associated copulatory mechanism; ultimately these structures are so advanced as to become subordinal characters.

MATERIALS AND METHODS

This revision is largely based on specimens I collected during several trips to South America and one to eastern Panama. Whenever possible, embiids encountered in the field were cultured as a means of securing ample series of adults for research and distribution to other museums.

As the first stage of a species description, I describe the holotype and then the characters of the allotype and other specimens before me. Only topotypic adults—usually from the holotype's culture—are designated as paratypes.

I drafted the illustrations from KOH-cleared

specimens mounted on microscope slides. Separate images in each plate are not always drawn to the same scale. Thickness of line and nonstippled shading reflect degrees of sclerotization. Membranous or fleshy areas are stippled. Only significant vestiture is indicated. Labrum is omitted in head figures.

Terminalia symbols are defined as follows: 9 = ninth abdominal tergum, 10 L and 10 R = hemitergites of tenth abdominal tergum, 10 LP and 10 RP = processes of these hemitergites, MS = medial sclerite of 10, MF = medial flap of 10, EP = epiproct (segment 11), ED = ejaculatory duct, H = hypandrium (sternum 9), HP = process of H, LPPT and RPPT = left and right paraprocts, LCB and RCB = left and right cercus-basipodites. Wing veins and sinuses are abbreviated as follows: C = costa, Sc = subcosta, ScBS = subcostal blood sinus, R = radius, RBS = radial blood sinus, Rs = radial sector, MA = anterior branch of media, MA1 and MA2 = branches of MA, MP = posterior branch of media, Cu = cubitus, CuA = anterior branch of cubitus, CuBS = cubital blood sinus, A = anal, ABS = anal blood sinus.

The following institutional abbreviations are used throughout the manuscript: AMNH = American Museum of Natural History, New York; BMNH = British Museum (Natural History), London; CAS = California Academy of Sciences, San Francisco (the author's collection); ICNB = Instituto de Ciencias Naturales, Bogotá, Colombia; IZAM = Instituto de Zoologia Agricola, Maracay, Venezuela; MIUP = Museo de Invertebrados, Universidad de Panamá, Panamá; MHNP = Museo de Historia Natural, Lima, Peru; MNR = Museu Nacional Rio de Janeiro, Brazil; MZSP = Museu do Zoologia, Universidade do São Paulo, Brazil; USNM = U.S. National Museum of Natural History, Washington, D.C.

Systematic Treatment

Family Clothodidae Enderlein

Clothodinae Enderlein, 1909:175 (subfam. of Embiidae); Enderlein 1912:21.

Clothodidae Tillyard, 1937:251.—Davis 1940*a*:536; 1940*b*:678; 1942:111.—Ross 1944:404.—Denis 1949:741.—Kaltenbach 1968:4.

Type genus.—*Clothoda* Enderlein, 1909, by original monotypy.

Distribution.—Amazon basin, northern South America, Trinidad, eastern Panama.

Diagnosis.—Males: Usually large but in a few species small. Coloration diverse. Wings always present; all veins well cuticularized, venation varying from most complete within order (MA always forked and CuA multibranched) to simple embioid type with CuA simple and few crossveins. Mandibles strongly apically dentate; submentum always sclerotic and inflexed on anterior and lateral margins. Hind basitarsi always with two ventral papillae. Abdominal terminalia highly symmetrical, varying from almost perfect symmetry in *Clothoda* to primitive asymmetry in other genera; tenth tergal processes undeveloped or, at best, short, simple lobes; paraprocts often equal, well sclerotized, but lacking processes or nodules; segments of left cercus identical to those of right cercus, never lobed or echinulate.

Females: Without unique family-level characteristics. Hind basitarsi always with two ventral papillae. Genitalia without pronounced lobes or sclerotizations.

Biology.—Species of this family occur in forests (or semicleared forest) of the Amazon, Orinoco, and Magdalena River basins, as well as in Trinidad and eastern Panama. Colonies usually are on tree bark (Fig. 1), rock ledges, and road banks. There is generic variation in appearance of the silk galleries. In *Clothoda* and *Antipaluria* they are fully exposed. In *Cryptoclothoda* and *Chromatoclothoda* they are covered with pulverized feces, debris, or micro-plant growth and thus are often difficult to find even when likely habitats are closely scrutinized.

Eggs are laid in single-layer clumps attached to a surface within the galleries. With her mandibles, the parent female deliberately places finely masticated material in and around the egg mass as it is laid. This protection, together with guarding by the parent, reduces oviposition by parasitic wasps. Nymphs develop in unison in a one-year cycle. They are highly tolerant of one another under crowded conditions within field and culture galleries.

Key to Genera of Clothodidae Males

1. Terminalia with paraproct sclerites (LPPT and RPPT) equal, or almost equal 2
— Left paraproct (LPPT) much larger than right (RPPT) 3
2. Terminalia with caudal apex of tenth tergum (MF) curled dorsad, tenth tergum (10) at best indistinctly cleft; epiproct (EP) small, inconspicuous. Head with gula bearing two

FIGURE 1. Colony of *Clothoda longicauda* Ross, new species, on trunk of rain forest tree near Tingo María, Peru. Apparently galleries of broods of two parent females have united. Occasionally, galleries of successive generations will completely envelope such trunks.

setal tufts anteriorly behind submental suture ..... *Clothoda*

— Apex of tenth tergum not curled dorsad; instead, it is broadly cleft forming two definite, similar, caudal lobes that are globose and coarsely setose dorsally; epiproct large, its sclerite conspicuous. Gula without setal tufts ..... *Cryptoclothoda*

3. Body sclerites uniformly dark (except in *caribbeana*); large, robust. Wing vein CuA at least two-branched (except in anomalous specimens); cross-veins numerous. Left

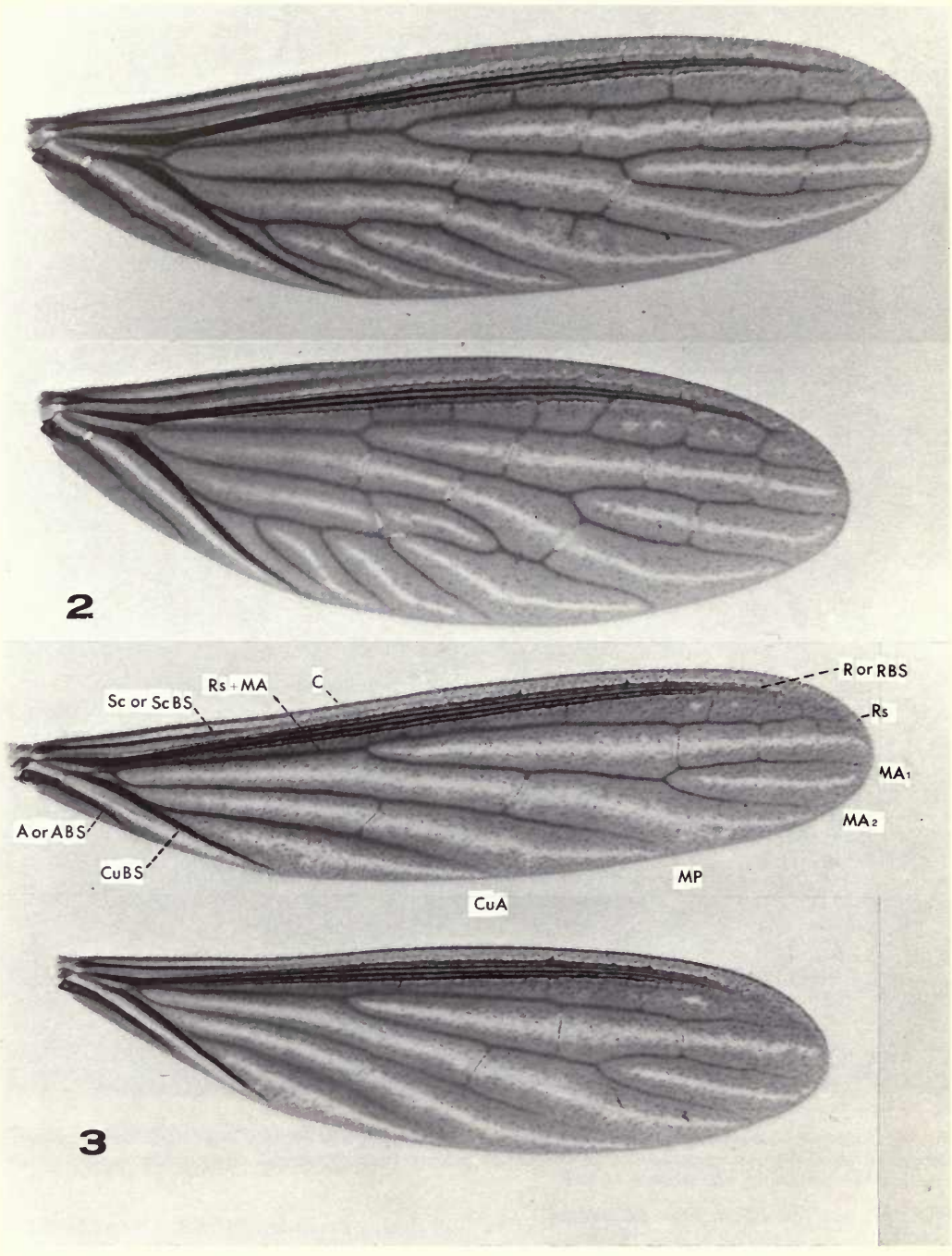


FIGURE 2. *Clothoda longicauda* Ross, new species, wings of paratype male. MP of hindwing is anomalous. Multibranched Cu is characteristic of *Clothoda*. FIGURE 3. *Chromatoclothoda albicauda* Ross, new species, wings of male from Mera region, Ecuador. A more distal forking of MA and the simple Cu characterize species of the genus *Chromatoclothoda*. For an explanation of symbols, see page 10.

hemitergite (10 L) with well-developed process (10 LP). Silk galleries conspicuous, not covered with pulverized material ..... *Antipaluria*

— Body sclerites multicolored (thorax entirely or partially golden); size medium to small, slender. Wing vein CuA always unbranched; few cross-veins (Fig. 3). Left hemitergite without a distinct, narrow process. Silk galleries inconspicuous, covered with pulverized material that at times supports microplant growth ..... *Chromatoclothoda*

Genus **Clothoda** Enderlein

Clothoda Enderlein, 1909:176; 1912:21.—Navás 1918:109 (tribe Clothodinos).—Tillyard 1937:250.—Davis 1939:373; 1942:111.—Ross 1944:404.

TYPE SPECIES.—*Embia nobilis* Gerstaecker, 1888, by original designation.

DISTRIBUTION.—South America: Amazon basin.

DIAGNOSIS.—Males: Very large, robust; alate; uniformly blackish brown. Cranium with mahogany, semitranslucent area between eyes, otherwise lacking pattern. Eyes small. Mandibles short, triangulate with coarse apical dentation; submentum sclerotic, sides inflexed and anteriorly convergent. Gular area with two tufts of setae immediately behind submentum. Prothorax robust, broader than head; concolorous with remainder of body. Wing veins strongly cuticularized to wing margin; CuA, and sometimes MP, branched at least once; cross-venation complex; costal margin white in type species. Hind basitarsi with two prominent, ventral papillae. Abdominal terminalia very symmetrical; tenth tergum uncleft, or only partially cleft; medial sclerite (MS) large and basally projected beneath ninth tergum (9); tergal apex (MF) elevated and curled basad; tergal processes either undeveloped, or at best, budlike; epiproct (EP) merely a fleshy, unsclerotized lobe beneath MF; ninth sternum (H) evenly but weakly sclerotized throughout, abruptly projected caudad as a symmetrical, medial process (HP) which is slightly cleft and microsetose at apex (ED); left and right paraproct sclerites (LPPT and RPPT) elongate, equal in size, convergent along sides of HP; left and right cercus-basipodites (LCB and RCB) similar, sclerotized dorsally only; left and right cerci equal, segments very elongate, evenly sclerotized, distal segment never pale.

Females: With coloration paralleling that of males but with distal antennal segments abruptly white. Body somewhat flattened, prothorax exceptionally broad, but otherwise without important generic anatomical characters.

COMPONENT SPECIES.—*Clothoda* is here restricted to its type species, *C. nobilis* (Gerstaecker 1888), which appears to be widespread in the mid and lower Amazon basin, and also a very distinct new species occurring in the Peruvian tributary region of the Amazon. Other species previously assigned to the genus are here placed in the genus *Antipaluria* Enderlein. The Tertiary fossil *Embia florissantensis* Cockerell (1908), placed in *Clothoda* by Davis (1939), has been assigned to the new genus *Lithembia* Ross (1984) because its wing venation is not of the *Clothoda* type and there is no evidence for placement in a Recent genus.

Key to Species of *Clothoda* Adult Males

1. Costal margin of wings cream-white; tenth abdominal tergum completely sclerotized except for small membranous area anterior to its upturned apex (MF). Antennal segments VIII–XVI ventrally bearing dense clumps of short, truncate setae. Lower and middle Amazon region of Brazil ..... *nobilis*

— Costal margin of wings blackish-brown; tenth abdominal tergum weakly cleft, membranous on left side of upturned apex (MF). Ventral setae of antennal segments VIII–XVI normal, not short and peglike. Montaña region of Peru ..... *longicauda*

Clothoda nobilis (Gerstaecker)

(Figure 4)

Embia nobilis Gerstaecker, 1888:1.

Embia (Olyntha) nobilis Krauss, 1899:148.

Olyntha nobilis (Gerstaecker) Krauss, 1911:31.

Clothoda nobilis (Gerstaecker) Enderlein, 1909:176; 1912:22, fig. 4–6, pl. 1, A–B.—Navás 1918:109, fig. 6.—Davis 1939:373, fig. 1–7.—Ross 1944:406.

NEOTYPE (BY PRESENT DESIGNATION).—Male, McLachlan Collection, BMNH. Data: "Itaituba (Amazonas)," Brazil.

Gerstaeker's type specimen is apparently lost. It is not in the Zoologisches Museum, Humboldt-Universität zu Berlin where Gerstaeker's collections presumably were deposited. I found no trace of it in any other museum.

His type specimen was from Itaituba, and it is likely that it and the neotype, as well as a male (labelled *Olyntha brasiliensis* Gray, possibly by

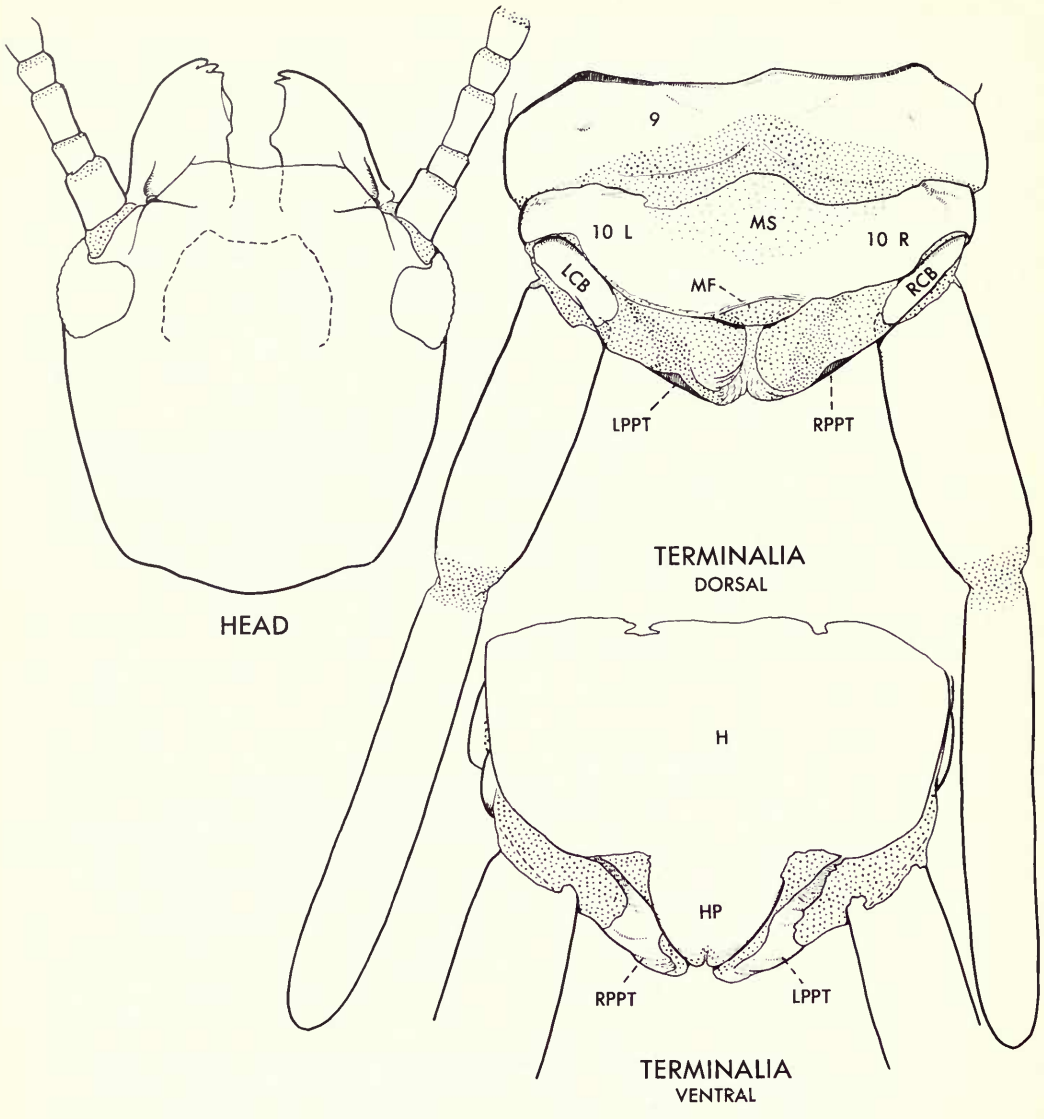


FIGURE 4. *Clothoda nobilis* (Gerstaecker). Head and terminalia of a male from Manaus region, Brazil. For an explanation of symbols see page 10.

Krauss) in the Naturhistorisches Museum, Vienna, were collected by H. W. Bates and divided among his clients.

McLachlan's specimen was described by Davis (1939) and I tentatively designated it lectotype (1944). However, because it was not studied by Gerstaeker, it cannot be considered a lectotype.

I have collected and reared extensive series of this remarkable species from the Manaus region, as well as Serra do Navio, Amapá, northeastern Brazil. The biology of *C. nobilis* is similar to that described for *C. longicauda* new species of the upper Amazon.

Adult males are easily distinguished by globose antennal segments that are largest in the medial portion of the antennae. Eight of these submedial segments (VIII–XVI) bear dense, ventral clumps of peculiar, short, truncate setae. The costal and

anal wing margins are whitish, and the terminalia are unique in that they lack medial cleavage of the tenth abdominal tergum. The apex of the tergum, however, is curled dorsad, and this apex probably is homologous to the medial flap which, in more apomorphic genera, becomes diagonal, or longitudinal, in position and attaches to the inner margin of the right hemitergite. Tergal surfaces on either side of the flap eventually evolve into left and right hemitergal processes in other species of the order.

Additional Old Record.—Brazil: Fonte Boa (Amazonas), two adult males and one adult female, Enderlein Collection, Instytut Zoologiczny, Warsaw.

New Records.—All Amazon basin, Brazil: Reserva Ducke, 25 km N Manaus; large colony on trunk of remnant tree in semi-cleared virgin forest, males matured 14-X through 31-XII-64 (Ross). Twenty km N Manaus, colonies common on tree trunks in yard of farmhouse, males matured 18-VIII through 5-X-65 (Ross). Serro do Navio, Amapá; colony on tree trunk in virgin forest, males matured during every month of 1964 but mostly during January, 1965 (Ross). Porto Platon 21-II-64; 1 female on bark (Lacombe). Casa do Sette, Amapari R.; one adult female, underside of house 19-II-65 (Lacombe). Ponte da Bolivia, Amazonas, 20-X-60; one adult male, three nymphs (Evangelista). All in CAS collection.

Clothoda longicauda Ross, new species

(Figures 1, 2, 5)

Holotype.—Male, on slide, CAS. Data.—Peru: 3 miles (5 km) W Tingo María, Huánuco, X-54 (Ross).

Description.—Appearance: very large, uniformly dark brown, including wing margins, but with whitish-tan antennal apices. Color details (in alcohol): cranium dark chocolate-brown; darkest in clypeal region, becoming lighter brown caudally and ventrally; vertex between eyes with large, golden, transverse spot. Eyes dark lavender-brown. Basal antennal segment blackish, other segments dark brown with white joint-membranes; two distal segments tan apically, white basally; antepenultimate segment medium brown apically, tan basally (complete antenna 20-segmented). Clypeolabral membranes pale lavender; labrum dark brown; mandibles dark mahogany; other mouthparts various shades of dark-to-medium brown. All body sclerites and legs essentially dark brown with golden-brown areas, especially ventrally; all body membranes dark lavender. Wings appearing dark brown with strong violaceous luster; hyaline intervals very narrow; costal and radius borders dark; cross-veins numerous, white when crossing hyaline intervals. Abdominal terminalia dark brown basally, caudal extremities tan to whitish (in membranes); cerci uniformly light brown. Dimensions (on slide): Body length 18.0 mm; fore wing length 11.2 mm, breadth 3.0 mm.

Important anatomical characters: Cranium short, broad; surface slightly depressed behind pale central spot; two shallow, sublateral carinas extend from inner curve of eyes and parallel lateral margins of cranium; medial stem of ecdysial suture finely carinate; cranial surface minutely reticulate but coarsely rugulose caudally in symmetrical pattern; gula, just behind tentorial pits, bearing two prominent clumps of dense, dark setae. Medial antennal segments without ventral, peglike setae. Abdominal terminalia relatively small, narrow; cerci exceptionally long, basal segment as long as apical; medial area of tenth tergum extensively membranous, almost completely cleft to apex; tergal processes not actually developed but precursors are evident; epiproct, as in *C. nobilis,* a small membranous lobe without a sclerite; paraprocts almost equal, the left slightly broader than the right.

Allotype.—Female (in alcohol) with holotype data and disposition.

Description.—Appearance: Large, robust, uniformly blackish-brown with dark membranes except for pale cranial spot and white apical segments of antennae. Color details: dull black except for transverse, rectangulate, golden area between eyes; antennal segments I–XVIII dark brown, remainder cream-white except for tan tip of segment XXIII (apical). All dorsal body sclerites blackish-brown with a faint green to purplish luster; ventral sclerites mostly mahogany-brown; all body membranes dark lavender. Legs essentially concolorous with body except for chestnut-brown femur-tibial joints and much of basitarsi of fore and mid legs. Apical segment of cerci medium brown blending to tan at apex. Prothorax exceptionally broad, as wide as cranium. Abdominal apex narrow and small; genital sternites and valvifers without notable features. Body length: 20.0 mm.

Paratypes.—Hundreds of reared adults from cultures collected in the immediate vicinity of Tingo María; in AMNH, BMNH, CAS, MHNP, and USNM.

Discussion.—Males of *Clothoda longicauda* are readily distinguished from those of *C. nobilis* by their more slender form, pale cranial spot, absence of peglike setae ventrally on medial antennal segments, entirely dark wing margins, more extensively cleft tenth abdominal tergite, and longer segments of cerci.

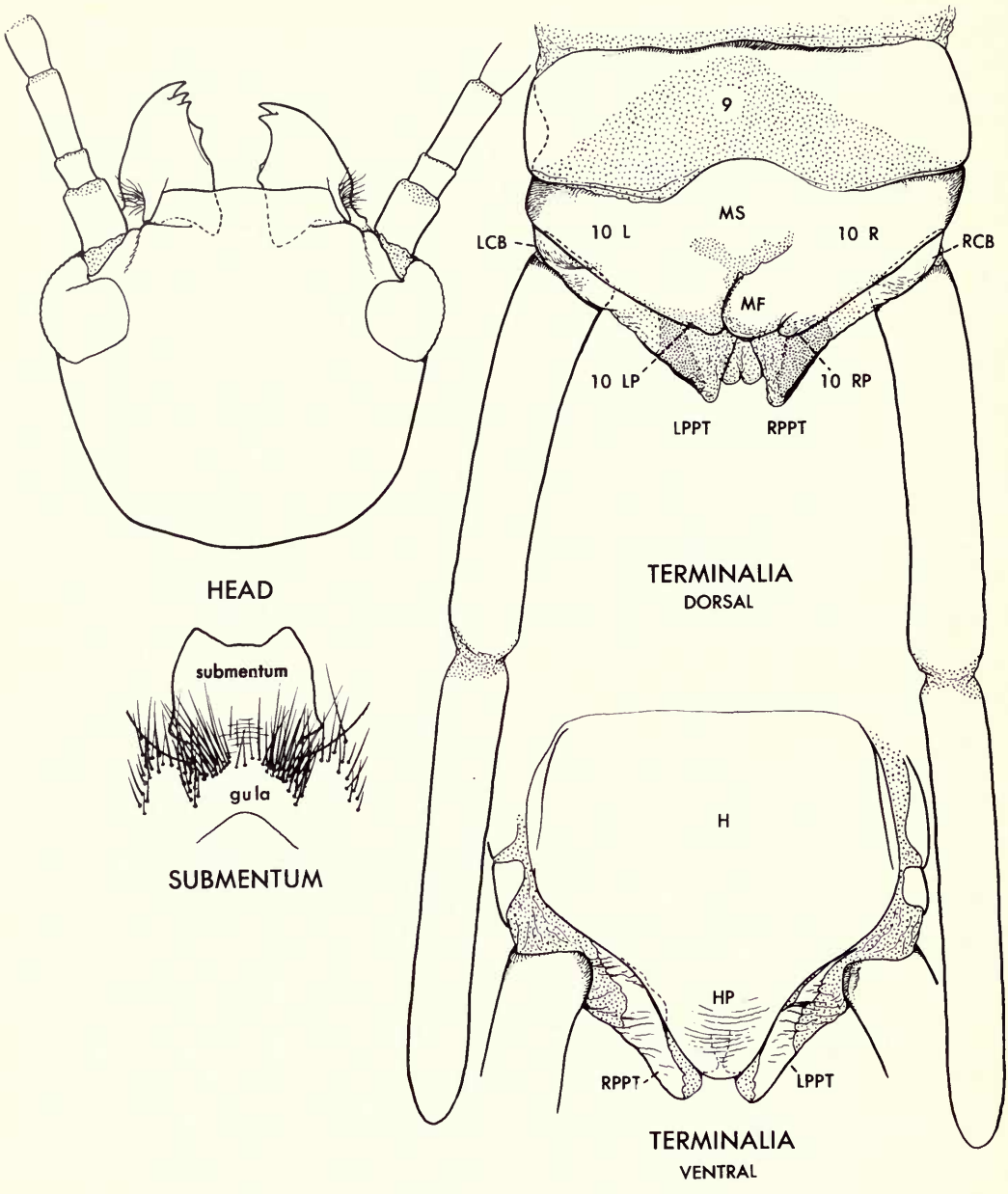


FIGURE 5. *Clothoda longicauda* Ross, new species. Head and terminalia of holotype. For an explanation of symbols see page 10.

Slight differences from locality to locality suggest that races may have differentiated.

BIOLOGY.—As in *Clothoda nobilis,* colonies of *C. longicauda* are rare and widely dispersed in virgin forest. Occasionally, however, a particular tree—usually a standing dead tree with rough bark—is almost completely enveloped by exposed, interconnected, white, silk galleries. Trees adjacent to such a concentration tend more frequently to have at least one small, pioneer colony.

The largest concentrations of *C. longicauda* (in fact, of all embiids) are found in partially culti-

vated areas adjacent to natural forest. Especially rich are new coffee plantations where some of the original forest trees remain standing to provide shade. Here, stumps, fence posts with bark still attached, as well as living trees, are common habitats. Occasionally, *C. longicauda* also occurs on surfaces of mossy rocks and old road or trail banks.

The gallery silk is fully exposed, white, and without a powdery cover of masticated material. Some galleries lead into protective crevices, but most colonies are entirely superficial, the layers of silk affording the same protection to galleries beneath as a layer of bark. The eggs are laid in a single-layer patch in a matrix of masticated material. Early-stage nymphs produce their own gallery systems beneath the cover of older galleries. Nymphs of both sexes are reddish-brown with white-tipped antennae. Adult males and females matured in greatest abundance in cultures during October and November, but it is possible that generations overlap and that adults may be encountered in the field at any time of the year.

The species is parasitized by a large, undescribed species of Sclerogibbidae, as well as by the tachinid fly *Perumyia embiaphaga* Arnaud, 1963.

Locality Records (all eastern Peru).—Boquerón de Padre Abad, Huánuco; colony on rocky ledge, males matured during XI-54. Yurac Plantation, Loreto (67 mi [108 km] NE Tingo María); colonies on tree trunks, males matured mostly during X-54. Yarina Cocha, Pucallpa, Loreto; colonies on tree trunks, males matured X-54. Two mi (3 km) W San Ramon, Junín; colonies on stumps in coffee plantation, males matured VII-55 through X-55. Collected by me and deposited in CAS.

This, or related species of *Clothoda,* were unsuccessfully sought (in habitats similar to that of the type series) in the Madre de Dios region of Peru, the Napo-Pastaza region of Ecuador, and the upper Putumayo region of Colombia.

Cryptoclothoda Ross, new genus

Type Species.—*Cryptoclothoda spinula* Ross, new species.
Distribution.—Brazil: Lower Amazon (one record).

Diagnosis.—Males: as large as, or larger than, those of *Clothoda,* alate, uniformly blackish-brown except for contrasting golden prothorax. Cranium without translucent, paler area between eyes; sides straighter and more caudally convergent than in *Clothoda*; gula without two anterior setal tufts. Eyes large, inflated; length almost equal to that of sides of head behind eyes. Antennae with segments of distal half very elongate; all segments bearing long, wavy setae; without ventral peg-setae. Mouthparts as in *Clothoda.* Prothorax narrower than head, golden-yellow; thorax and legs narrower than in *Clothoda.* Wings with vannal area narrowly tapered, caudal margin straight (curved in *Clothoda*); all veins strongly marked, broader than in *Clothoda* and most other embiids; CuA unforked. Hind basitarsi as in *Clothoda.* Abdominal terminalia with tenth tergum broadly cleft medially (almost to base of tergum), forming almost equal hemitergites that are depressed and almost devoid of setae just before production of caudal processes; left process (10 LP) smaller than right, short, thumblike, well sclerotized, upper surface bristling with numerous short setae; right process (10 RP or MF) equal in length to 10 LP but broader and submembranous on inner-apical side, dorsal surface densely setose, setae short and directed laterad and caudad; epiproct (EP) large with dark, sclerotic, rodlike sclerite. Ninth sternum (H) symmetrical, evenly sclerotized; its process (HP) centered, symmetrical, short, apex rounded, membranous except for a narrow sclerotized medial area. Paraprocts (LPPT and RPPT) very similar, left only slightly broader, each narrowly attached to sides of H. Cercus-basipodites (LCB and RCB) obsolete. Cerci perfectly symmetrical.

Females: Without important generic characters.

Component Species.—Only the type species is known, but others may be expected in the vast Amazon basin.

Discussion.—*Cryptoclothoda* is somewhat intermediate between *Clothoda* and *Chromatoclothoda.* It is more *Clothoda*-like in the great symmetry of its abdominal terminalia, especially that of its processes, hypandrium, and paraprocts. However, *Cryptoclothoda*'s galleries, like those of *Chromatoclothoda,* are very cryptic, being not fully exposed and detritus-free, as are those of *Clothoda* and *Antipaluria.* It differs from *Chromatoclothoda* in being much larger, more robust, and in having a more distinctly developed left tergal process and a less-developed left paraproct.

It is probable that both tergal processes are actually homologs of the medial flap. If so, in this genus the flap is cleft into two almost identical "processes." The left becomes the diverse left tergal process characteristic of almost all embiids, while the right is homologous to the medial flap of most embiids. The right tergal process of such embiids appears to derive from the caudal angle of the right hemitergite.

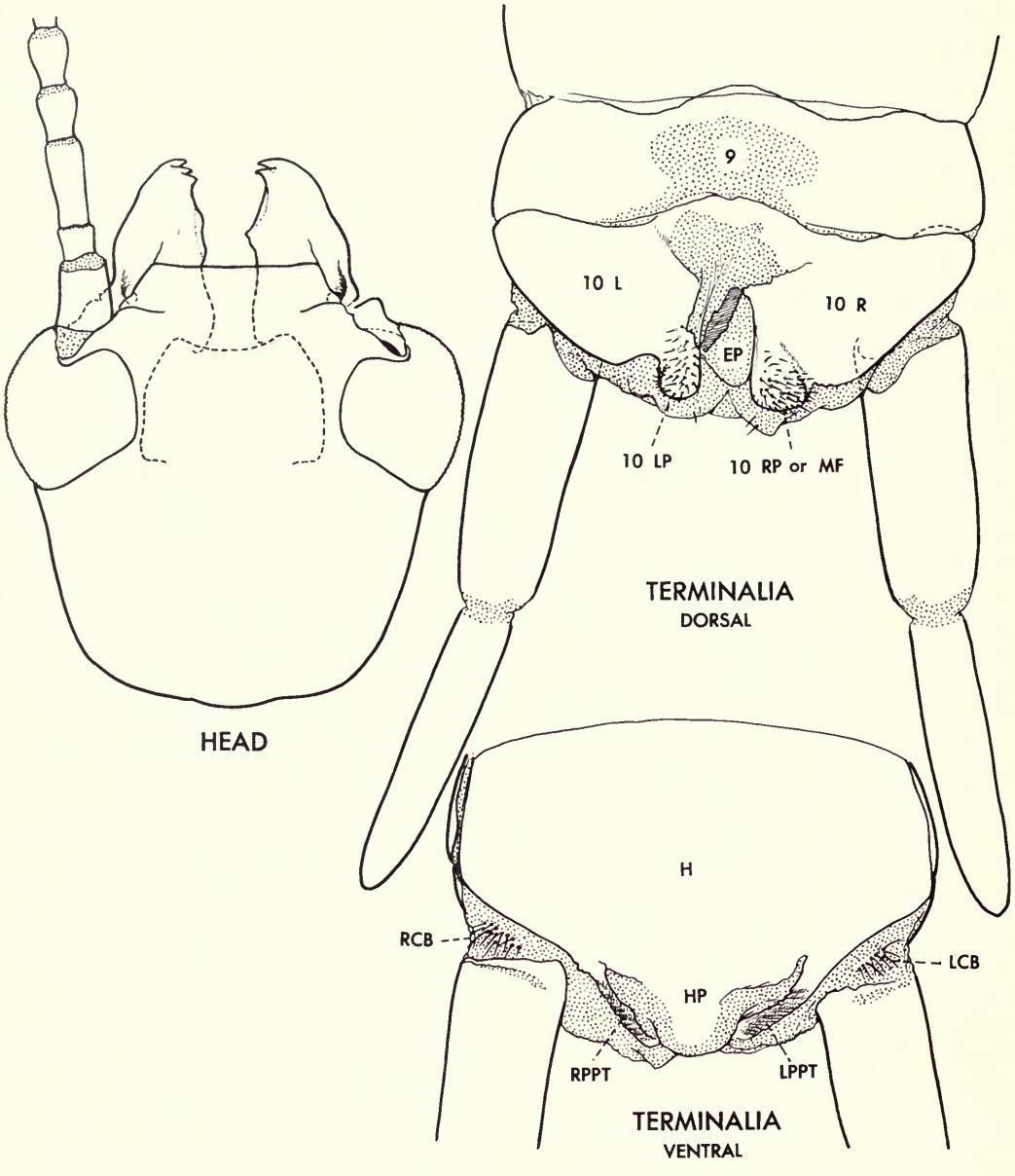


FIGURE 6. *Cryptoclothoda spinula* Ross, new genus and species. Head and terminalia of holotype. For an explanation of symbols see page 10.

Cryptoclothoda spinula Ross, new species
(Figure 6)

HOLOTYPE.—Male, on slide, CAS. Data.—Brazil: 50 km N Paragominas, Pará; silk gallery in bark crevices of recently felled tree in virgin forest. Matured in culture 28-V-75 (Ross).

DESCRIPTION.—Appearance: Very large, as large as *Clothoda nobilis,* alate; generally blackish except for contrasting golden prothorax; antennae and cerci entirely blackish, legs entirely blackish except for tan on sides of hind femora. Color details (in alcohol, freshly killed): Cranium dark chocolate-brown with matte luster; raised, shiny, transverse, medial, dark amber area between eyes; tentorial pit areas yellow-amber; gu-

lar bridge and margins of foramen magnum amber. Eyes pale purple with narrow, whitish outline. All antennal segments shiny black with pink membranes; 21 segments present, terminals broken off during capture, but these were also black. Preclypeal and labral membranes pink; labrum blackish. Mandibles dark amber with piceous dentation. Maxillae pale amber except for blackish palpi. Labium blackish except for amber mentum and piceous anterior margins of submentum. Cervical and prothoracic sclerites translucent yellow (except caudal angles of pronotum); all associated membranes almost concolorous, except for rust-yellow subdermal tinge. Pterothorax largely pale straw-yellow dorsally with symmetrical light brown clouding; sternites various shades of brown, adjacent membranes tinged rust-red. Legs various shades of brown except for tan areas on hind femora; mid and hind coxae dark gray-tan. Wings generally dark with narrow hyaline intervals; in sidelight the pigment bands appear brilliant metallic purple and the veins metallic cobalt-blue; granular borders of RBS very pale pink. Abdomen with basal terga light brown, terga IX and X blackish-brown; all dorsal membranous areas salmon-pink except for cream pleural fold of segments I–VI; ventral sclerites tan except for mahogany-brown sides, terminal segments becoming darker, hypandrium and paraprocts blackish-brown with associated membranes reddish. Cerci very dark brown with joint membrane reddish. Dimensions (on slide): body length 17.0 mm; fore wing length 12.0 mm, breadth 3.0 mm.

Important anatomical characters (Fig. 6): Head with distinctively large eyes. Terminalia highly symmetrical with unusual tenth tergal processes. These are short, rounded, globose with numerous, stiff, short setae; right process (10 RP or MF) almost twice as broad as left (10 LP).

Allotype.—Female, in alcohol, with same data and disposition as holotype (from same field colony), killed 31-X-75, failed to mate with holotype and thus unable to lay fertilized eggs.

Description.—Appearance: Large, robust; various shades of dull, mahogany brown with white antennal apices and cream-white dorsopleural abdominal membranes. Color details: Cranium dark chestnut-brown except for frons and medial area of clypeus which are dark mahogany-brown; lateral areas of clypeus golden-brown. Eyes lavender-black. Antennal segments I–XXIII shiny-black, segments XXIV–XXVI (the apical) white with purple joints. Anteclypeal and labral membranes white, tinged with purple. Submentum, mentum, palpi, labrum, and mandibles dark mahogany-brown. All other sclerites golden-brown. Cervical area pale purple. Pronotum mottled mahogany-brown; clouded with yellow-tan medially, forming indefinite, pale, longitudinal stripe. Meso- and metathorax mottled, dull mahogany-brown; with subcutaneous, pale clouding on promontories of meso- and metascuta, metascutum darker than mesoscutum and with purplish luster. All thoracic membranes lavender. Legs various shades of chestnut- and mahogany-brown dorsally; ventral surfaces of coxae, trochanters, and femora of mid and hind legs shades of pale yellow; distal tarsal segments pale. Abdomen concolorous with thorax but less dull in luster; segments I–VII with distinct, subcutaneous, cream, dorsopleural membranes forming pale, longitudinal, bordering lines; distal segments darker brown, especially laterally on paragenital sternites; all ventropleural and paragenital membranes purple. Cerci uniformly dark mahogany. Body length (in alcohol): 19.0 mm.

Biology.—Nymphs of the type pair were collected in virgin rain forest on 27-II-75. Their silk galleries were difficult to detect, being partially covered by vines growing up the trunk of a large forest tree that had been recently pushed over to make an access road for timber removal. When the tree was standing, the galleries would have been at least 50 feet (15 m) above ground level but it is doubtful that the species is confined to upper trunk levels. Probably many nymphs were present on the tree but their galleries were almost impossible to find because of dense epiphytes. I spent several days fruitlessly searching for additional colonies but found none, nor did I find the usually conspicuous galleries of *Clothoda*.

Late in May, 1975, the two nymphs matured in culture as a male and a female. They were kept alive together for a period that seemed sufficient to insure mating. However, after five months, when the female had failed to lay eggs, she was killed and preserved. It is assumed that she had failed to mate. In spite of this, the two individuals are unquestionably conspecific, probably siblings.

Antipaluria Enderlein

Antipaluria Enderlein, 1912:63.—Navás 1918:106.—Davis 1939:373 (as syn. of *Clothoda* Endl.).—Ross 1944:411 (as syn. of *Clothoda* Endl.).

Type Species.—*Antipaluria aequicercata* Enderlein, 1912, by original designation.

DISTRIBUTION.—Northern South America, Trinidad and eastern Panama.

DIAGNOSIS.—Males: Similar to those of *Clothoda* except as follows. Gula with setae uniformly distributed, without two anterior clumps. Antennae without ventral peg-setae. Abdominal terminalia completely cleft to base; medial sclerite (MS) obsolete, its area entirely membranous; left hemitergite with distinct but small caudal process (10 LP) projected from inner margin is often membranous on inner side; and up-turned right process (10 RP or MF) short, triangulate, somewhat fleshy (this process may be derived from medial flap (MF) which is otherwise absent); epiproct (EP) developed as short flap between hemitergites, its sclerite well sclerotized but narrow; ninth sternum (H) broader than long, caudal angles gradually converge to form broad-based, short, medial process (HP), which is asymmetrically membranous on caudal margin and not terminally cleft as in *Clothoda;* left paraproct (LPPT) as in *Clothoda,* but shorter and broader at apex; right paraproct (RPPT) reduced to a narrow sclerotic fragment fused to basal margin of HP; left and right cercus-basipodites (LCB and RCB) dorsally obsolete; each represented lateroventrally by sclerotic fragment, or setose membranous area; left and right cerci perfectly symmetrical, segments shorter than in *Clothoda,* apical segments usually concolorous with basals but at times paler.

Females: Without significant generic characters. Unlike those of *Clothoda,* membranous areas often pale, forming distinctive pattern, especially pale lines along the upper pleurae of the abdomen.

DISCUSSION.—Because of the great superficial resemblance to *Clothoda,* and the conformity of many characters, *Antipaluria* was not recognized by Davis (1939) or myself (1944). Now that I have studied both genera in the field and laboratory and have discovered several new species, I am convinced that *Antipaluria* is distinct in many ways, such as the absence of two setal tufts anteriorly on the gula, the well-developed tenth tergal cleft and processes, the well-developed epiproct and its sclerite (rudimentary in *Clothoda*), and the asymmetrical paraprocts.

The seven species in my collection (CAS) may be assigned to three groups, as follows: (1) the Aequicercata Group, males of which have a narrow, evenly sclerotized left tergal process; (2) the Urichi Group with the left tergal process sclerotized only on its left side and the antennal apices white; (3) the Marginata Group with left tergal process as in the Urichi Group but with antennae uniformly dark and the wings white-margined. When northern South America is thoroughly surveyed for embiids, many additional species should be discovered. In combination with geographic occurrence, adult males of the known species may be distinguished as follows.

Key to Species of *Antipaluria* Males

1. Costal margins of wings whitish. Apical antennal segments dark. Colombia, east of Andes (Marginata Group) ..... *.marginata*
— Costal margins of wings dark. Apical antennal segments whitish 2
2. Epiproct sclerite (EP) curved, rather broad, its base not contacting inner side of right hemitergite (10 R) (Aequicercata Group). 3
— Epiproct sclerite straight, very slender, its base contacting inner side of right hemitergite (Urichi Group) 4
3. Left mandible broadly arcuate between apical dentation and molar cusp. Left tergal process (10 LP) very narrow, sides sclerotized except at extreme apex. Colombia W of Andes ..... *.aequicercata*
— Left mandible with a large, acute flange in above-mentioned position. Left tergal process broad basally, gradually tapered; sides and apex desclerotized. Panama E of Canal ..... *.panamensis*
4. Clypeus flat, anterior margin straight. Trinidad ..... *.urichi*
— Clypeus vaulted medially, anterior margin emarginate on either side of this promontory. Venezuela 5
5. Thorax unicolorous brown. Caracas region ..... *.intermedia*
— Prothorax entirely or partially golden or amber-yellow 6
6. Cervical sclerites dark. Pronotum dark except for golden to amber-yellow caudal third. Tropical mountain forest, Rancho Grande .. .. *.silvestris*
— Cervical sclerites and prothorax entirely golden-yellow. Lowland, coastal forest .... *.caribbeana*

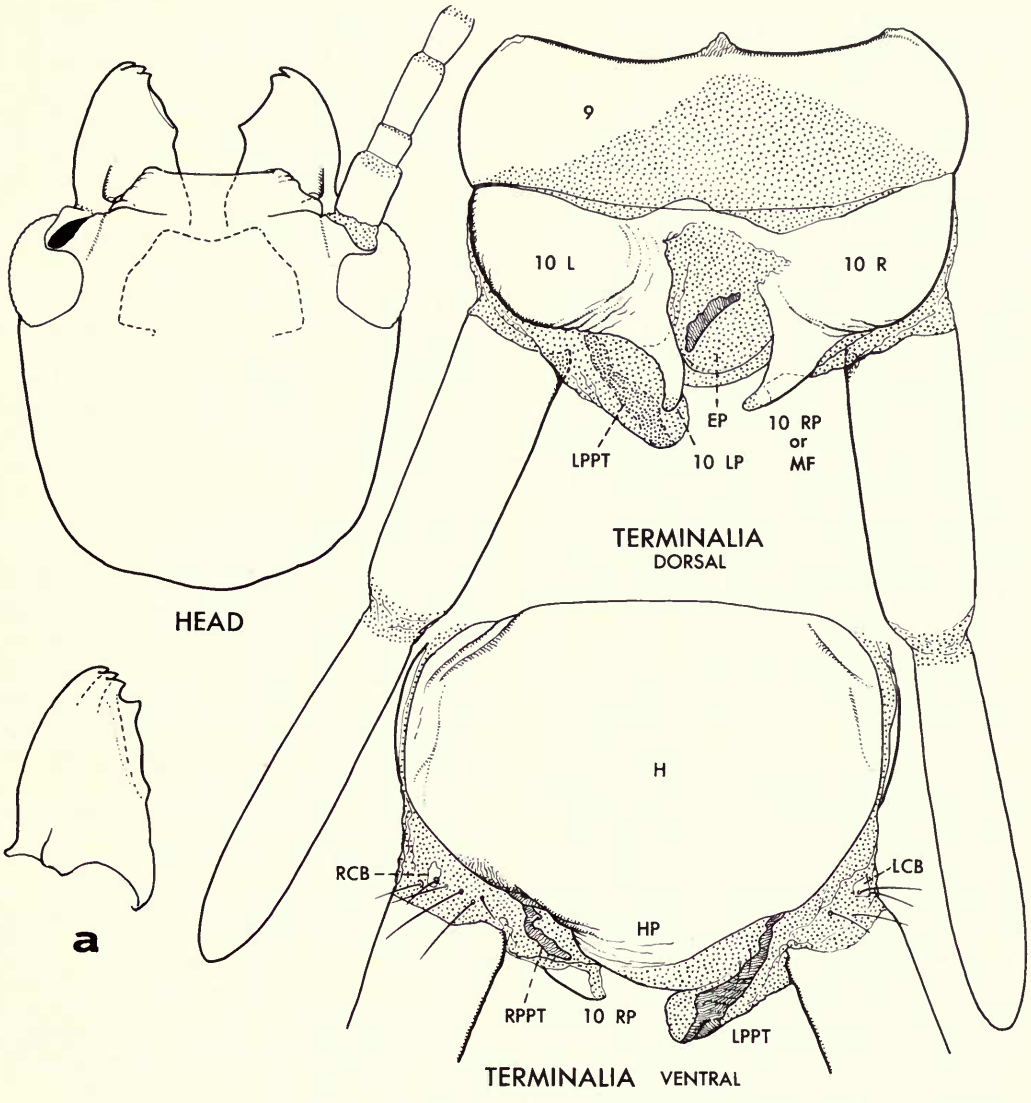


FIGURE 7. *Antipaluria aequicercata* Enderlein. Head and terminalia of neotype. For an explanation of symbols see page 10. Figure 7a. *Antipaluria panamensis* Ross, new species. Left mandible of holotype.

The Aequicercata Group

Antipaluria aequicercata Enderlein

(Figure 7)

Antipaluria aequicercata Enderlein, 1912:63.—Navás 1918:107.—Matsuda 1960:718, pl. I, fig. 5, 6 (anatomy of thorax).

Clothoda aequicercata (Enderlein) Davis, 1939:379.—Ross 1944:410, fig. 10–13.

NEOTYPE (BY PRESENT DESIGNATION).—Male, on slide, CAS. Data.—Colombia: 3 mi (5 km) E Guadas, Cundinamarca, 1240 m, 3-III-55 (Ross). From colony on shaded, mossy road bank.

Enderlein's unique type, an adult male with damaged terminalia collected by Moritz, was labeled "Columbien." It was deposited in the "Berliner Zoologischen Museum (Kat. Nr. 2734)." According to Dr. St. von Kéler, who loaned me types of other Enderlein species in this museum (now Zoologisches Museum, Humboldt-Universität zu Berlin), the type specimen of *A. aequicercata* is lost; also because this species is the type of a genus, and had no specific type locality

within Colombia, the present designation of a neotype is justified.

DESCRIPTION (OF NEOTYPE).—Appearance: Large (body length 18 mm); blackish-brown throughout except for white antennal apices and dark, metallic-blue wing luster. Cranium relatively small, greatest width behind eyes equal to broadest portion of prothorax; surface finely alutaceous dorsally, less so on gular surface; dull black without trace of pattern; surface very shallowly, broadly depressed behind fork of ecdysial suture; surface immediately before this junction transversely elevated as broad, medially depressed, smooth, shining "V"; behind extremity of each ecdysial sutural branch, flat, ocelluslike spot visible, but these lack ocellar structure. Clypeus with complete, deep suture between the tentorial pits; medial area flat, or shallowly depressed; anteclypeal and labral membranes dull smoke-black. Eyes black, shining. Antennal segments glossy black except for four white distals with amber extremities; terminal segment apically gray; 24-segmented; segments elongate, rounded distad, narrowly tapered caudad, membranes purple-black; setae erect, elongate, wavy. Mandibles piceous, rugose; form as figured. Other mouthparts blackish-brown. Submentum form as figured, piceous with a deep, broad, elongate depression on each side; all margins strongly reflexed and elevated. All sclerotized portions of thorax and legs, including first acrotergite, uniformly black, shining except on alutaceous surfaces; all membranes dark gray-white, scarcely contrasting with sclerites. Dark areas of wings blackish-brown with bluish luster, all margins dark; hyaline intervals narrow, cross-veins white only when crossing these intervals. All sclerotized portions of abdomen, including terminalia and cerci, shining jet-black; membranes and medial areas of eighth and ninth terga purple-black. Dimensions (freshly killed): Body length 18.5 mm; fore wing length 11.5 mm, breadth 2.9 mm.

Important anatomical characters (Fig. 7): flat clypeus; obtuse, rather than acute left mandibular flange between apical dentation and molar cusp; narrow, well-defined, left tergal process (10 LP) with abruptly membranous tip; acute right process (10 RP); detached epiproct sclerite.

NEOALLOTYPE.—Female with neotypic data and disposition.

DESCRIPTION.—Large, robust. All sclerotized dorsal surfaces glossy blackish-brown with faint purple luster except for dull, alutaceous black cranium with faint mahogany "cloud" between eyes. Antennal coloration parallels that of males. Most body membranous areas dull, dark lavender, appearing concolorous with sclerites to unaided eye. However, some dorsal membranous areas whitish in consistent pattern as follows: white dorsocoxal membrane of forelegs; transverse yellow-white band across front margin of meso- and metascuta, forming two prominent pale thoracic bands; dorsopleural areas of first eight abdominal segments abruptly white, combining to form white line down each side of abdomen. Mid and hind coxae and trochanters pale yellow; terminal segments of cerci gray-tan. Ventral sclerites of body clouded with medium brown. Body length 27.5 mm.

PARANEOTYPES.—Hundreds of adults reared in type culture; deposited in AMNH, BMNH, CAS, ICNB, IZAM, MIUP, and USNM.

ADDITIONAL RECORDS.—Colombia: 5 mi (8 km) E El Colegio, Cundinamarca, 1370 m, 9-III-55 (ROSS); 18 mi (29 km) W Honda, Caldas, 820 m, 16-III-55 (Ross).

DISCUSSION.—*Antipaluria aequicercata* is probably confined to tropical forests of the western drainage of Colombia. A closely related species, described below, occurs in rain forest of eastern Panama. These two species can most readily be distinguished from other congeners by their slender, well-formed left tergal process.

BIOLOGY.—*Antipaluria aequicercata* produces conspicuous silk galleries on tree trunks, stumps, and other surfaces in mountain rain forests. Much of this zone in Colombia is devoted to coffee production. Several other embiid species also occur on residual trees, stumps, and fence posts in coffee plantations. In culture, males of *A. aequicercata* mature almost every month of the year. Because of the abundance of the species, it seems safe to conclude that Moritz's type specimen, labeled "Colombia," was collected in one of the easily accessible coffee regions of the country. This seems to justify the present choice of a neotype from a coffee-growing locality. The specimen described by Ross (1944) closely resembles the neotype and is from the neotype region. However, its exact origin is uncertain because it was collected at a U.S. port among orchids in plant quarantine shipped from Medellín, Colombia.

Antipaluria panamensis Ross, new species
(Figure 7a)

HOLOTYPE.—Male, on slide, CAS. Data.—Panama: 10 km N El Llano, Panama 1300′ elev., matured in culture 17-XII-76 (Ross).

DESCRIPTION.—Appearance: Large, relatively

slender; blackish-brown throughout, including membranous areas, except for white-tipped antennae and lavender wing luster. Color (in alcohol) and anatomical details: Cranium rather small, narrow, caudally tapered; vertex between eyes with two raised, amber elevations; surface otherwise alutaceous, dull blackish-brown clouded with mahogany. Clypeus transversely depressed; anterior margin straight, inflexed, sclerotic. Antennal segments elongate; bearing long, erect, wavy setae; blackish blending to dark mahogany; segment XXI tan, blending distad to cream; XXII–XXIV whitish, the terminal (XXV) white, tipped with brown. Palpi concolorous with antennal bases. Submentum translucent mahogany, short, broad; broadly depressed on each side. Prothorax narrower than cranium across eyes; pronotum dark mahogany with paler areas along lateral margins and sutures; all other sclerites, including cervicals, dark mahogany; all membranes dark lavender, not contrasting with tone of sclerites. All other body sclerites and legs various shades of mahogany-brown with dark lavender membranes, appearing unicolorous black to unaided eye. Wings very dark, almost black, hyaline intervals narrow with diffuse margins; wing margins dark; cross-veins with white portions small, indistinct; setae relatively long. Terminalia very similar to *A. aequicercata* especially in narrow, definite form of 10 LP; 10 RP, however, shorter and much less acute. Dimensions (on slide): Body length 16.5 mm; fore wing length 11.7 mm, breadth 2.6 mm.

ALLOTYPE.—Female, in alcohol, with same data and disposition as holotype.

DESCRIPTION.—Larger and more robust than males. Very similar to females of *A aequicercata* but smaller and less robust with body sclerites more blackish and apparently with greater purple luster. Transverse, pale, thoracic bands whiter and less broad (especially that associated with mesonotum). Body length: 21.0 mm.

PARATYPES.—Numerous adults reared in type culture. Deposited in AMNH, BMNH, CAS, ICNB, IZAM, MIUP, and USNM.

DISCUSSION.—*Antipaluria panamensis* is closely related to *A. aequicercata,* but males are distinct in many minor characters such as the following: smaller size and more slender proportions, especially the elongate cranium; the left mandible bears an acute projection between the dentation and its proxadental cusp (a broad, low flange in *A. aequicercata*); broader, shorter submentum; the tenth tergal processes are less sclerotized in *A. panamensis,* 10 RP being much shorter and broader. Females may be distinguished by characters mentioned in the neallotype description.

The occurrence of a clothodid on the isthmus of Panama was unexpected. During October, 1976, after much search in the low, virgin rain forest at the type locality, I found only two colonies. Each was the brood of a single female that produced a conspicuous labyrinth of fully exposed, white galleries on the trunk of a small tree. During December 1976, nymphs were penultimate, and most males and females matured in culture during January, 1976, and as late as March. No second brood was reared because of a *Diplocystis* infestation. I am indebted to Dr. Lynn Siri Kimsey, who collected a female of this species on 3-IV-74 and thus called my attention to its occurrence, and to Dr. Robert Dressler for taking me to Dr. Kimsey's collection site.

The Urichi Group

Antipaluria urichi (Saussure), new combination
(Figure 8a)

Embia urichi Saussure, 1896*a*:293.

Olyntha urichi (Saussure) Krauss, 1911:29, pl. 1, fig. 2, 2a (ex parte, included potential type of *A. aequicercata*).

Antipaluria urichi (Saussure) Enderlein, 1912:64.—Navás 1918:106.

Clothoda urichi (Saussure) Davis, 1939:377, fig. 17–21; 1942:111, fig. 1–5.—Ross 1944:406, fig. 8.—Mc. C. Callan 1952:483.—Kirkpatrick 1957:79, 267.

Embia uhrichi Saussure (*lapsus calmi*), 1896*b*:350.—Melander 1903:103, fig. 2c.—Friederichs 1906:238.—Kershaw 1914:24, pl. 3, 4 (embryology).

Cotypes.—Pinned males, Muséum d'Histoire Naturelle, Geneva. Data.—"Insula Trinitaris (Antillae), a Dom. Uricho lecta" (probably Port of Spain).

DISTRIBUTION.—This species is common throughout Trinidad, where its colonies are especially conspicuous on trunks of shade trees in settled areas. It also is sporadically distributed on trees, stumps, etc., in natural forest. For the present, it is best to regard the species as limited to Trinidad. Specimens from Caracas, Venezuela, determined as *Clothoda intermedia* Davis, 1939, and later identified by him (1942) as *urichi,* represent a distinct species.

RECOGNITION.—Any clothodid found in Trinidad may be considered to be *A. urichi.* Adult males differ from those of all known Venezuelan species by their very flat clypeus with a straight an-

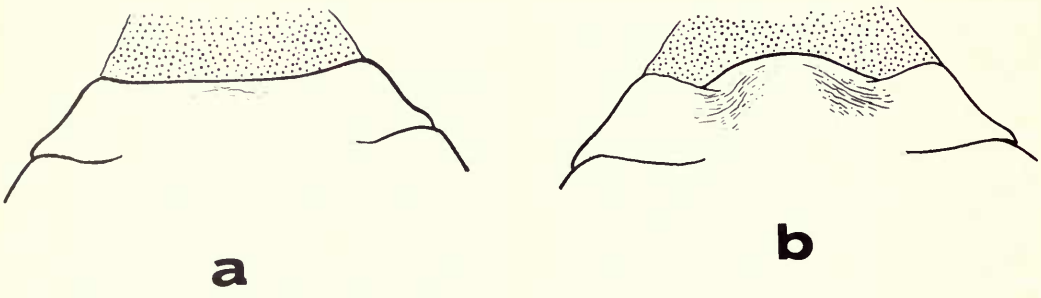


FIGURE 8a. *Antipaluria urichi* (Saussure). Clypeus of male from Trinidad. Figure 8b. *Antipaluria intermedia* (Davis). Clypeus of topotypic male.

terior margin (Fig. 8a). It is probable that *A. urichi* occurs naturally on adjacent shores of Venezuela, and there is always the possibility that its range has been extended by human commerce. Numerous Trinidad records in the literature and in my collection (CAS) need not be cited because of the small size of the island.

This species has been the subject of recent, intensive, behavioral studies by Janice Edgerly.

Antipaluria intermedia (Davis), new combination (Figure 8b)

Clothoda intermedia Davis, 1939:376, fig. 8–16; 1942:112 (as syn. of *A. urichi*).

Clothoda urichi intermedia (Davis), Ross, 1944:408, fig. 6, 7, 9, pl. 18, A.—Mc. C. Callan 1952:483.

HOLOTYPE.—Male on pin (damaged in transit to museum), BMNH. Data.—Venezuela: Caracas (Dr. Ernst).

DISCUSSION.—In the British Museum I located a few adult males of *A. intermedia,* in alcohol with type data, which apparently were not studied by Davis. One of these specimens is now in CAS by exchange.

On the basis of previously overlooked characters, it is apparent that *A. intermedia* is distinct from *A. urichi* of Trinidad. Most significant, as shown in Figure 8b, is the strongly vaulted, glossy, piceous-black medial area of the clypeus (flat in *A. urichi*) and consequent bi-emarginate anterior clypeal margin (straight in *A. urichi*). My Ernst specimen is large (body length 20.5 mm), robust, and all sclerites are uniformly brown (probably lightened from blackish-brown by long preservation in alcohol). Inasmuch as the following two closely related new species demonstrate that coloration characters are consistent, it would be desirable to study the coloration of freshly collected specimens from Caracas.

For the present, males of the following three species can be superficially distinguished by pronotal and cervical coloration. That of *A. intermedia* apparently is uniformly dark brown; *A. silvestris* has blackish cervical sclerites, and the posterior third of the otherwise dark pronotum is yellowish whereas all cervical and prothoracic sclerites of *A. caribbeana* are golden. Such coloration is consistent in hundreds of males. Probably there are also reliable anatomical characters; for example, the left mandible of *A. silvestris* is more deeply emarginate on either side of the medial flange and the clypeus is not as prominently domed as in *A. intermedia.*

Antipaluria silvestris Ross, new species

HOLOTYPE.—Male, on slide, CAS. Data.—Venezuela: 10 km N Rancho Grande (near Maracay). 8-III-75 (Ross).

DESCRIPTION.—Appearance: Large, slender; all sclerotic surfaces blackish except for golden-brown posterior third of pronotum; cervical and prothoracic membranes white, other body membranes dark lavender except for whitish dorsopleural abdominal membranes; four apical antennal segments abruptly whitish. Color (in alcohol) and anatomical details: Cranium small, elongate, jet black, dull; postocular surface depressed; interocular ridge dark, glossy. Clypeus rugose, transversely strigose medially on a surface which is broadly elevated; anterior margin weakly arcuate. Antennal segments mostly globular with short, straight setae. Eyes almost as dark as cranium. Sclerotized portions of mouthparts only slightly lighter than cranium; submentum rugose, deeply foveate. Cervical sclerites very dark brown, membranes white. Pronotum blackish-brown but blending at about caudal third from golden-brown to amber-yellow; anterior mem-

branous margin narrowly yellow; other prothoracic sclerites blackish-brown. Sclerotized portions of body and legs various shades of dark brown, thoracic scuta clouded with golden-brown; all such surfaces reflecting a bluish luster. Tenth tergal processes fleshy, strongly curled dorsad; inner sides membranous. Epiproct sclerite very slender. Terminalia generally similar to that of *A. caribbeana*. Dimensions (on slide): Body length 15.0 mm; fore wing length 11.0 mm, breadth 2.75 mm.

ALLOTYPE.—Female, in alcohol, with holotype data and disposition.

DESCRIPTION.—Essentially as in *A. aequicercata* but with distinct distribution of white in membranous regions of body as follows: all dorsal, intersclerotal membranes white except those anterior to the thoracic scuta, and the pleural and sternal membranes, which are lavender (thus the characteristic, transverse prescutal white bands of *A. aequicercata* are absent); membrane above forecoxae dark lavender. Apical segments of cerci and most of mid and hind coxae, golden-tan. Body length: 20 mm.

PARATYPES.—Many adult males and females reared in holotype culture. Deposited in AMNH, BMNH, CAS, ICNB, IZAM, MIUP, and USNM.

DISCUSSION.—Males of this species may be recognized by their slender body form, dark coloration, and especially, by the bicolorous pronotum (blackish with posterior third blending to yellow). The fact that the species was collected only a few kilometers inland from the habitat of *A. caribbeana* suggests that many additional species of *Antipaluria* will be discovered as northeastern South America is thoroughly searched for embiids.

The type culture was collected on a vegetation-draped rocky roadbank in high, tropical cloud forest a short distance north of the crest of the pass between Maracay and Ocumare de la Costa (10 km N Rancho Grande). The vegetation was distinct from that of the deciduous thorn forest habitat of *A. caribbeana*. There is also approximately a 700-m difference in altitude between the two type localities.

Antipaluria caribbeana Ross, new species

HOLOTYPE.—Male, on slide, CAS. Data.—Venezuela: near Ocumare, inland from Turismo, almost at sea level. Matured in culture 10-VII-75 (Ross).

DESCRIPTION.—Appearance: Large, robust; blackish-brown throughout with faint bluish luster except for the yellowish prothorax and white antennal apices. Cranium oval, eyes exceptionally small and forward. Clypeus very short, abruptly slanted ventrad; medial area vaulted, heavily sclerotized, jet black, glossy, transversely striated; anterior margin arcuate. Cranial surface dull piceous except for small golden area between eyes which is elevated as small, transverse, glossy ridge. Gula pale amber, glossy. Antennae entirely dark except for four whitish apical segments, most basal of which is pale tan; setae rather short and somewhat recumbent. Submentum slightly produced at apical angles; basal angles deeply foveate, apparently containing residue of whitish secretion. Sclerites of prothorax and cervix amber-yellow, tinged, especially along sutures, with brown; all adjacent membranous areas cream-white. Remainder of body and appendages piceous-brown with bluish luster. Numerous white cross-veins in wings. Terminalia similar to *A. urichi* but with inner side of 10 LP more extensively membranous; 10 RP shorter, less acute, apex rounded. Segments of cerci shorter, more robust. Dimensions: Body length 17.0 mm; fore wing length 11.0 mm, breadth 2.6 mm.

ALLOTYPE.—Female, in alcohol, with data and disposition same as the holotype.

DESCRIPTION.—Much larger than males. All sclerotized areas blackish-brown and all membranous areas whitish. Cranium with large, transverse golden-brown area between eyes occupying at least one-third surface of head. Antennae dark brown except for four, entirely white, distal segments. Prothoracic and cervical sclerites dark brown, pale ventrally, associated membranous areas whitish, subcutaneously lavender at sides and ventrally. All other body segments similar in coloration except posterior pronotal plate and lighter brown legs; dorsopleural membranes of thorax with pure white, subcutaneous, fat globules resulting in dorsopleural stripe running almost full length of each side of body. Tarsi becoming light brown. Body length 24.0 mm.

PARATYPES.—Hundreds of topotypic, culture-reared males and females in AMNH, BMNH, CAS, ICNB, IZAM, MIUP, and USNM.

DISCUSSION.—*Antipaluria caribbeana* eventually may prove to be but a subspecies of poorly known *A. intermedia* from the Caracas region. Males of the two species have in common the small-eyed, oval cranium; the complex clypeus; the deeply foveate submentum; and much else. Although the type localities of the two species are

in the same general region, it is assumed that altitudinal and ecological differences (Caracas region, above 1000 m and Ocumare near sea level) would be reflected in at least subspecific differences in many components of the respective biotas. For the present, *A. caribbeana* is immediately recognizable by the contrasting pale color of the prothorax and cervix.

BIOLOGY.—The type cultures of *A. caribbeana* were collected in conspicuous galleries spun on surfaces of rocky road banks. Each colony consisted of a single female and her brood of nymphs that had found refuge from desiccation and predation in galleries penetrating rock cracks.

The small hills and canyons of the Ocumare environment are clothed with a dense tangle of large trees, thorny shrubs, and lianas. During my visit in March, the weather was dry, and thus most of the vegetation was leafless. Adults matured in cultures during July, and by the first of August oviposition began. The egg masses were large and single layered. Toward the end of August, nymphs began hatching, and adults of these broods matured during April and May of the following year. It is thus likely that the species has only one brood per year.

The Marginata Group

Antipaluria marginata Ross, new species

HOLOTYPE.—Male, on slide, CAS. Data.—Colombia: 3 mi (5 km) W of Villavicencio, Meta, 920 m, III-55 (Ross).

DESCRIPTION.—Appearance: Large, robust; dull dark mahogany throughout (including entire antennae) except for cream-white membranous areas of body and whitish costal and anal margins of wings. Anatomical and color (in alcohol) details: Cranium relatively small, elongate, sides straight; surface finely alutaceous dorsally, smooth ventrally, pattern obsolete; with two glossy foveae between eyes. Clypeus transversely striate, glossy; medial area vaulted; anterior margin bi-emarginate. Eyes rather small, forward in position. Antennae, including membranes, uniformly dark brown to apex; flagellar segments globose, 24 in number; setae rather short, curved, not wavy. Mandibles glossy piceous with dark amber areas; left mandible with an acute tooth between apical dentation and molar cusp. Submentum largely yellow-amber, piceous anteriomedially; very deeply foveate in caudal angles. All sclerotized portions of body and legs uniformly dark brown except for pale posterior pronotal plate and pale femur-tibial joints of mid and hind legs; all membranous areas cream-white except for dark lavender tones of ventral pterothoracic membranes. Wings with pigmented areas dark brown, without bluish luster; costal margin, especially in basal half, translucent cream-white; hind margin whitish between base and apex of cubital sinus; cross-veins numerous, white when crossing hyaline intervals. Dimensions: Body length 17.0 mm; fore wing length 12.0 mm, breadth 2.85 mm. Terminalia: Broad, cerci stout, basically similar to those of *A. aequicercata* but with processes, especially 10 LP, less distinctly formed, somewhat fleshy, thick and short; epiproct sclerite (EP) detached, short, side margins obtusely angled; surface between tenth hemitergites and processes less depressed.

ALLOTYPE.—Female, in alcohol, with same data and disposition as the holotype.

DESCRIPTION.—About size of average male. Coloration similar to that of males but with a suffused, golden-brown, transverse area between eyes; antennae distinct due to five whitish apical segments (23 segments total). Body length: 17.5 mm.

PARATYPES.—Twenty-five topotypic adult males in CAS, ICNB, and USNM.

RECORDS.—All specimens were collected in the vicinity of Villavicencio (3 mi [5 km] W at 920 m; 8 mi [13 km] W at 1150 m; and 4 mi [6 km] SE at 410 m). Unfortunately, only a small series of adults was reared from these lots. Adult males appeared in culture between March and December; there is probably no definite period of peak maturation.

DISCUSSION.—*Antipaluria marginata* males may be distinguished at a glance by their white-bordered wings (similar to those of *Clothoda nobilis*) and the entirely dark antennae (no white tips). It is the only species of *Antipaluria* known from east of the Andes in Colombia. Related species are almost certain to be discovered as the eastern portions of Colombia are explored.

Antipaluria marginata is very common in the vicinity of Villavicencio and its galleries cover roadside fence posts, stumps, logs, and tree trunks so extensively that they can be seen from a moving vehicle. *Antipaluria marginata's* colony structure and habits are very similar to those described for *Clothoda longicauda.*

Chromatoclothoda Ross, new genus

TYPE SPECIES.—*Chromatoclothoda elegantula* Ross, new species.

DISTRIBUTION.—Amazon basin.

DIAGNOSIS.—Males: Small to large (body

length 9.3–15.5 mm). Body multicolored; prothorax, and at times entire thorax, yellow or orange; antennae and cerci often with distal segments white. General form more slender than that of other clothodids. Mandibles varying from stout *Clothoda* type to delicate, thin oligotomoid type; gula without setal clumps. Prothorax not exceptionally broad. Wings narrow with anal area strongly tapered and reduced; pigmented venal bands paler than in other clothodid genera with costal and RBS borders brighter pink, or red; all wing veins strongly cuticularized almost to apices; fork of MA more distal than in most clothodids; MP and CuA always unbranched; relatively few cross-veins. Hind basitarsi with two ventral papillae, medial one at times small. Abdominal terminalia generally as in *Antipaluria* but with mesocaudal angle of left hemitergite membranous and produced as a very short process, or not at all; right process (10 RP) scarcely produced. Ventral structures and cerci as in *Antipaluria.* Apical segments of cerci often contrastingly pale.

Females: Without important generic characters but differing from other clothodids in having the body surface very glossy, luster at times metallic. Antennal apices, and often apical segments of cerci, white.

Discussion.—*Chromatoclothoda* is a very interesting genus with increased specialization of characters, especially of the head, wings, and terminalia. The terminalia structure is closer to that of *Antipaluria* and *Cryptoclothoda* than to *Clothoda,* but the biology is strikingly distinct from that of these genera. Colonies are established on sheltered tree bark, especially undersides of horizontal tree branches, and rock ledges; colonies usually consist of long galleries that are apparently used repeatedly by successive generations. This is evidenced by the density and whiteness of the silk walls resulting from a long accrual of silk, layer on layer. The outer surfaces of such galleries are coated with finely pulverized bark or fecal material on which a cover of lichens or fine moss may grow. As a result, the colonies are very difficult to find. *Chromatoclothoda* egg masses are more sparsely enclosed in masticated material than those of *Clothoda* and *Antipaluria.*

Component Species.—Five new species have been collected in the Amazon drainage of Peru, Ecuador, Colombia, and Brazil. When other localities are visited, very careful search for the cryptic colonies should bring to light many additional species.

Key to Species of *Chromatoclothoda*
Adult Males

1. Apical segments of cerci white. Hemitergites of tenth abdominal segment without distinct processes 2
— Cercus segments uniformly dark. Hemitergites with small but distinct processes 4
2. Thorax entirely golden. Peruvian drainage of Amazon and middle Amazon basin 3
— Prothorax golden, pterothorax dark brown. Ecuadorian and Colombian tributary region of Amazon basin ..... *albicauda*
3. Sides of submentum feebly arcuate, gradually convergent anteriorly; anterior margin shallowly emarginate (Fig. 9). Coxae and trochanters as dark as other leg segments. Manaus region, Brazil ..... *elegantula*
— Submentum sides strongly arcuate; anterior margin narrowly and deeply emarginate (Fig. 9a). Coxae and trochanters of all legs golden. Tingo María region, Peru .... *aurata*
4. Larger species (body length 13 mm). Antennal apices dark. Upper Rio Perené, Peru ... . *nigricauda*
— Smaller species (body length 9 mm). Antennal apices pale. Huánuco region, Peru..... ..... *nana*

Chromatoclothoda elegantula Ross, new species
(Figure 9)

Holotype.—Male, on slide, CAS. Data.—Brazil: Reserva Ducke, 10 km N Manaus, Amazonas; matured in culture 14-VIII-64 (Ross).

Description.—Appearance: Medium sized (body length 13 mm), winged; blackish except for brilliant orange thorax, white-tipped antennae and distal segments of cerci. Color details (in alcohol): Cranium entirely piceous, almost black, except for suffused golden-brown gula and margins of occipital foramen. Eyes dark purple, tone paler than that of cranium; margins narrowly golden. Antennal segments I–XIV concolorous with cranium, with wavy piceous setae; segment XV apically gray; segments XVI–XX, including setae, white. Mandibles basally piceous, blending distad to dark red-amber; submentum red-amber; palpi and labrum blackish-brown, other mouthparts golden. Cervical and thoracic sclerites brilliant orange with contrasting blackish setae, all thoracic membranes concolorous with sclerites; mesospinasternum clouded with dark gray. Forecoxae and midcoxae basally yellowish, blending distad to black; hind coxae entirely black; all other leg

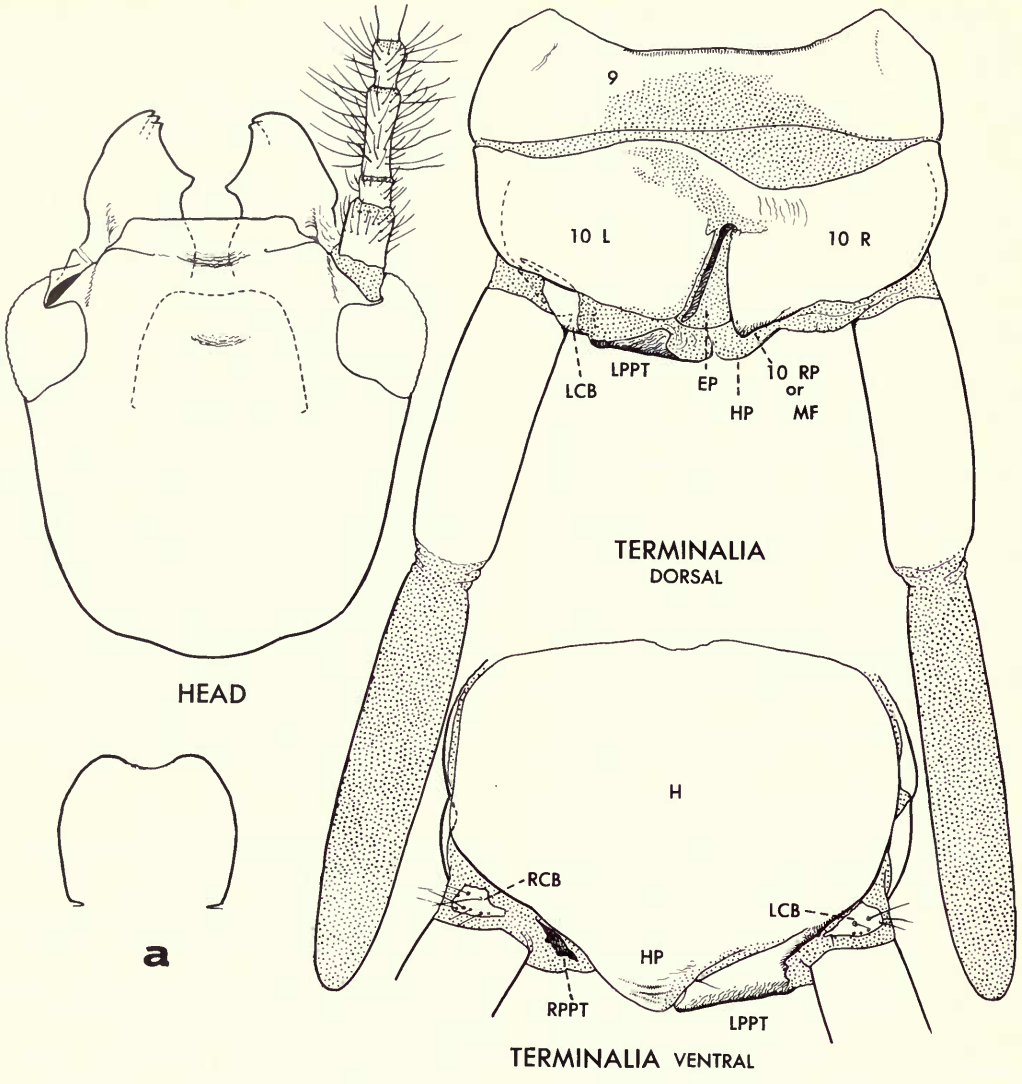


FIGURE 9. *Chromatoclothoda elegantula* Ross, new species. Head and terminalia of holotype. For an explanation of symbols see page 10. Figure 9a. *Chromatoclothoda aurata* Ross, new species. Submentum of holotype.

segments black. Wings richly pigmented; all longitudinal veins broad and dark; venal bands dark gray-brown; hyaline intervals light gray with weak margins; RBS borders brick-red. All abdominal sclerites blackish-brown with distal, submembranous band of each segment mottled rust-red; sclerotic areas of ninth and tenth segments darker, associated membranes tan, tinged with rust-red; apices of hemitergites as dark as bases, epiproct sclerite red-brown. Basal segments of cerci dark brown with membranous extremities rust-red; distal segments snow-white especially so because of white internal tissue, setae pale amber. Dimensions (on slide): body length 13.0 mm; fore wing length 8.0 mm; breadth 1.7 mm.

Important anatomical characters (Fig. 9): wings smaller and narrower than in closest relative, *C. aurata*; veins more heavily marked, MA branched well distad of midpoint; fewer crossveins between Rs and MA. Terminalia processes

not developed; inner margin of right hemitergite more sharply defined and sclerotized than in *C. aurata*. Epiproct sclerite (EP) very slender, narrowly linked to right hemitergite. Distal segments of cerci longer than basals and not sclerotized.

ALLOTYPE.—Female, in alcohol, with holotype data and disposition.

DESCRIPTION.—Appearance: Moderately large, cylindrical; glossy, jet-black except for white antennal apices and gray-white band across dorsum of joint between meso- and metathorax. Color details: Cranium dull, alutaceous blackish-brown suffused with golden-brown around anterior tentorial pits, sides of clypeus, and gula. Antennae 20-segmented, blackish except for 4 white apical segments. Prothoracic sclerites rather dull black with faint glint of dark blue, dark chestnut-brown ventrally, membranes lavender. Meso- and metathorax similar except for more dull texture of scuta and white membranes dorsally between segments. All legs concolorous with thorax but with anterior tarsi red-mahogany. Abdominal sclerites dark mahogany with surface smooth, shining, luster faintly greenish, intersegmental areas more reddish; all membranes purple. Sterna VIII and IX without unusual features. Cerci with basal segment dark, apical segment blending distad from medium brown to tan. Body length: 11.0 mm.

PARATYPES.—Numerous topotypic males and females. Adults matured in cultures between July and September. Deposited in CAS, USNM, BMNH, MNR, and MZSP.

DISCUSSION.—*Chromatoclothoda elegantula* of the middle Amazon is very closely related to *C. aurata* occurring in the Peruvian tributary region of the Amazon River, along Río Huallaga, near Tingo María. As series from intermediate localities become available, it is possible that *C. aurata* will prove to be indistinguishable. *Chromatoclothoda elegantula* can at present be separated from *C. aurata* by its more slender, elongate antennal segments (length four to five times longer than diameter); its submentum is broadest across the base and the sides are not evenly arcuate, and the inner margin of 10 RP is sharply defined (vague and submembranous in *C. aurata*).

BIOLOGY.—The type culture was propagated from several colonies found in the bark of large trees scattered in a small, roadside farm and from one colony in bark in virgin forest. The galleries were almost completely obscured by debris and a growth of lichens and moss. The silk of old galleries was very dense and white but freshly spun silk was quite transparent, lavender in tone, and finely dusted with pulverized fecal pellets.

Chromatoclothoda aurata Ross, new species
(Figure 9a)

HOLOTYPE.—Male, on slide, deposited in CAS. Data.—Peru: 5 mi (8 km) SW of Las Palmas (near Tingo María), Huánuco, about 1000 m, matured in culture 5-XII-54 (Ross).

DESCRIPTION.—Appearance: Large, very similar to *C. elegantula* but much larger; dark mahogany-brown with entire thorax golden-yellow; antennal and cercus apices white. Color details (in alcohol): Cranium very dark mahogany-brown with faint dorsal pattern; ventrally dark chestnut-brown. Eyes blackish-lavender, rimmed with golden-brown. Basal segment of antenna concolorous with cranium; segments II–XVI mahogany-brown; segment XVII basally tan, otherwise cream-white, segments XVIII–XXI pure white (segmentation complete). Mandibles piceous-brown; submentum similar, other mouthparts medium brown. Thoracic and cervical sclerites basically pale yellow, furca and basisterna paler; dorsal sclerites, especially pronotum, tinged with golden-brown; thoracic setae contrastingly dark brown; all thoracic membranes cream-white. Coxae of all legs pale yellow, trochanters tan, all other segments red-mahogany. Abdominal sclerites medium to dark brown; membranes gray-lavender, segments nine and ten and basal segments of cerci dark mahogany, the latter with dark lavender membranes at extremities of segment; distal segments of cerci pure-white with pale amber setae. Dimensions (on slide): Body length 17.5 mm; fore wing length 11.0 mm, breadth 2.75 mm.

Important anatomical characters: Very similar to *C. elegantula* but with minor distinctions, for example, antennal segments shorter (length less than three times segment diameter); submentum with evenly arcuate sides, broadest across middle; molar cusps of mandibles obtuse, less pronounced; inner margin of 10 RP weak, submembranous.

ALLOTYPE.—Female, in alcohol, data and disposition same as holotype.

DESCRIPTION.—Smaller than males. All sclerotized surfaces blackish-brown, body glossy, antennal and cercus apices white, pale band across apices of meso- and metathoracic scuta. Cranium dull, dark mahogany-brown with red-mahogany clouding between eyes and around tentorial pits. Eyes almost concolorous with cra-

nium. Antennae with segments I–XVII blackish-brown, XVIII blending to medium brown; remaining 5 segments cream-white, becoming paler distad. Legs glossy, blackish-brown, apices becoming dark tan. Most intersclerite membranes dark lavender except whitish dorsally between thoracic segments. Basal segments of cerci black, apicals whitish-tan. Body length 15.0 mm.

PARATYPES.—Three topotypic males and 28 adult females. Also, 30 males and 26 females from Cueva de la Pava, near Tingo María, Huánuco, Peru; matured in cultures between 10-IX and 24-XI-65 and 1 pair III-66, (Ross). Paratypes deposited in CAS, BMNH, and MHNP.

ADDITIONAL RECORD.—Peru: W end Boquerón de Padre Abad, Cordillero Azul (E Tingo María) 1 male matured III-24-55 (Ross).

BIOLOGY.—Matted galleries occur on the underside of slanted tree trunks, large and small, especially along margins of streams and in dark, shaded habitats.

Chromatoclothoda albicauda Ross, new species
(Figure 10)

HOLOTYPE.—Male, on slide, deposited in CAS. Data.—Colombia: Mocoa, Nariño, 700 m, 2-III-55 (Ross).

DESCRIPTION.—Appearance: Moderately large, winged; mahogany-brown with yellowish prothorax and white-tipped antennae and cerci. Color details (in alcohol): Cranium uniformly dull, dark mahogany-brown; lacking pattern; ventral surface and gula slightly paler. Eyes dark purple, margins narrowly golden. Basal antennal segment concolorous with cranium; segments II–XIII medium mahogany-brown, vestiture brown; XIV basally tan, apical two-thirds cream; XV–XIX white (antennae complete), vestiture white. Mandibles piceous-brown; submentum amber basomedially, otherwise varied shades of mahogany-brown to piceous; other mouthparts medium brown. Cervical and prothoracic sclerites basically yellow-brown; pronotum darker due to suffusion of golden-brown and dark brown setae; associated membranous areas cream-white. Pterothorax and abdomen mahogany-brown with piceous sutures; membranous areas purple-brown, same tone as sclerotic areas. All leg segments mahogany-brown except for yellow-brown fore coxae and trochanters; thoracic membranes mesad of hind coxae largely white. Wings medium brown, more or less concolorous with pterothorax and abdomen; hyaline intervals very narrow, margins well defined; all veins strongly cuticularized; cross-veins behind Rs white when crossing hyaline intervals. Sclerites of abdominal terminalia dark mahogany-brown, membranes rust-brown, apices of processes concolorous with hemitergites; basal segments of cerci, including their basal and distal membranes, dark mahogany-brown; distal segments white but with brown setae. Dimensions (on slide): body length 13.5 mm; fore wing length 9.5 mm, breadth 2.2 mm.

Important anatomical characters: Cranium elongate, sides parallel, abruptly rounded caudally. Mandibles with apical teeth close together, not clearly visible from dorsal aspect. Sides of submentum abruptly convergent distad. Left tergal process (10 LP) not produced, margins unsclerotized; right process (10 RP or MF) broadly acute, short. Other details as figured.

ALLOTYPE.—Adult female, in alcohol, with holotype data and disposition.

DESCRIPTION.—Coloration similar to *C. aurata* but lacking pale, membranous, dorsal band between pro- and mesothorax; however, such band present between meso- and metathorax. Membranous areas also pale around metascutum and abdominal tergum I. Basal segments of cerci very dark brown; distal segments medium brown, becoming pale distad. Body length 14.5 mm.

PARATYPES.—Nineteen topotypic males and 15 females reared in type culture. Deposited in BMNH, CAS, ICNB, and USNM.

ADDITIONAL RECORD.—Ecuador: 6 mi (10 km) W Mera, Napo-Pastaza VII-55 (Ross), deposited in CAS. Galleries on underside of rock ledge. Future studies may indicate that this population is at least subspecifically distinct from that of Mocoa, Colombia. Minor distinctions include paler wings due to broader hyaline intervals, a deep midclypeal fovea, and paler setae on the distal segments of the cerci.

Chromatoclothoda nigricauda Ross, new species
(Figure 11)

HOLOTYPE.—Male, on slide, CAS. Data.—Peru: Ridge above Colonia Perené, 18 mi (30 km) NE of La Merced, Junín. Matured in culture VI-55 (Ross).

DESCRIPTION.—Appearance: Moderately large, slender, alate; prothorax and dorsum of pterothorax bright orange, body and appendages otherwise blackish. Color details (in alcohol): Cranium jet-black throughout. Antennae black, grading distad to smoke-black; apical segments apparently not white (20 segments present, apparently complete); antennal setae wavy. Submentum piceous, palpi blackish-brown. Prothorax bright orange throughout with sclerite margins rust-brown. Fore coxae and trochanters similar in basal half blending to dark brown dis-

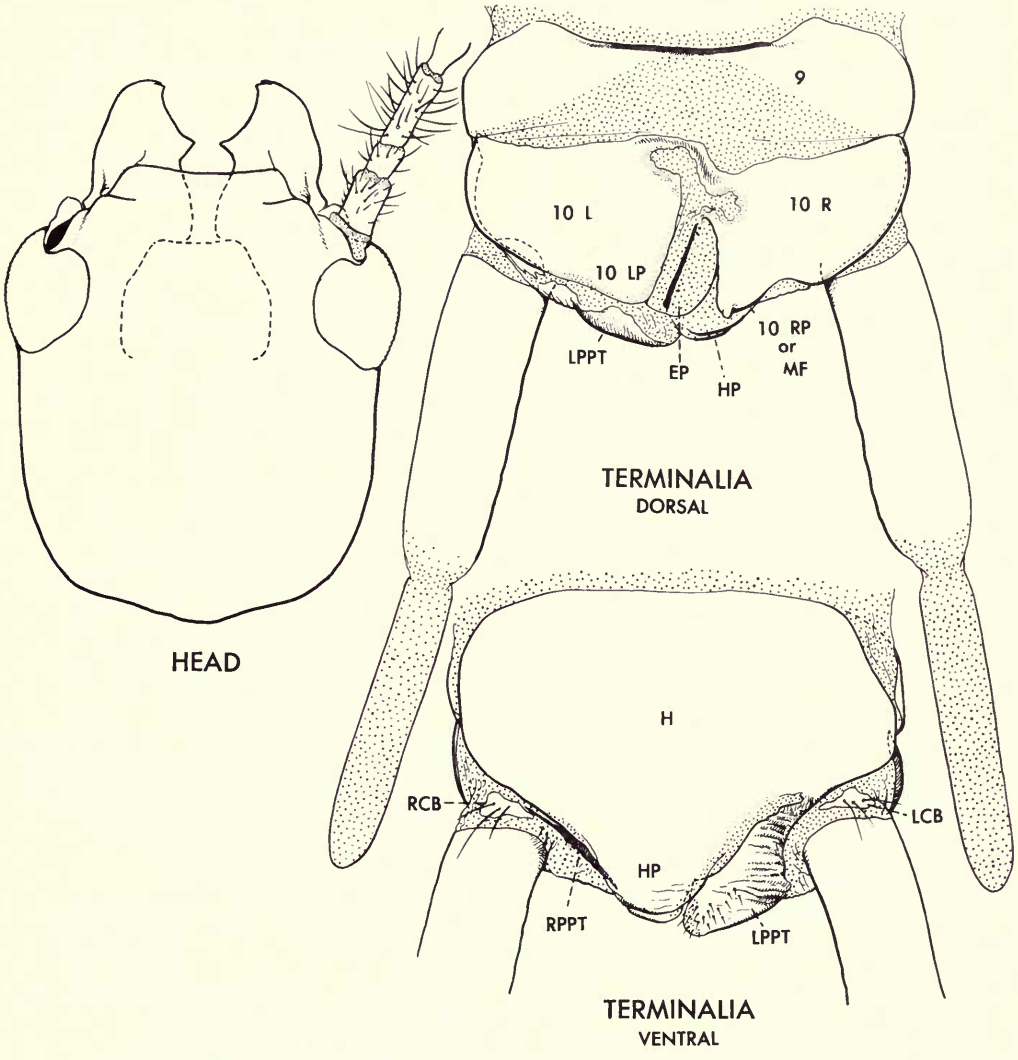


FIGURE 10. *Chromatoclothoda albicauda* Ross, new species. Head and terminalia of holotype. For an explanation of symbols see page 10.

tad; fore tibiae and tarsi piceous-black. Other legs similar but with tibiae and tarsi somewhat lighter. Pterothorax with scutae orange, margins and axillary cords rusty; pleurites and sternites dark brown. Axial area of wings orange. Abdomen dark piceous-brown with rusty membranes; terminalia sclerites and cerci piceous-black. Dimensions (on slide): Body length 11.7 mm; fore wing length 8.2 mm, breadth 2.0 mm.

Important anatomical characters: As in Figure 11.

Female: No specimens.

BIOLOGY.—The nymph of the holotype was found in chalk-white, dense, ribbonlike galleries amongst small vines on a dead stump in low, ridge-top forest. The galleries were inconspicuous due to a covering of fine debris.

Chromatoclothoda nana Ross, new species
(Figure 12)

HOLOTYPE.—Male, on slide, deposited in CAS. Data.—Peru: Yurac Plantation, 67 mi (108 km) E of Tingo María Huánuco, 14-XII-54 (Ross).

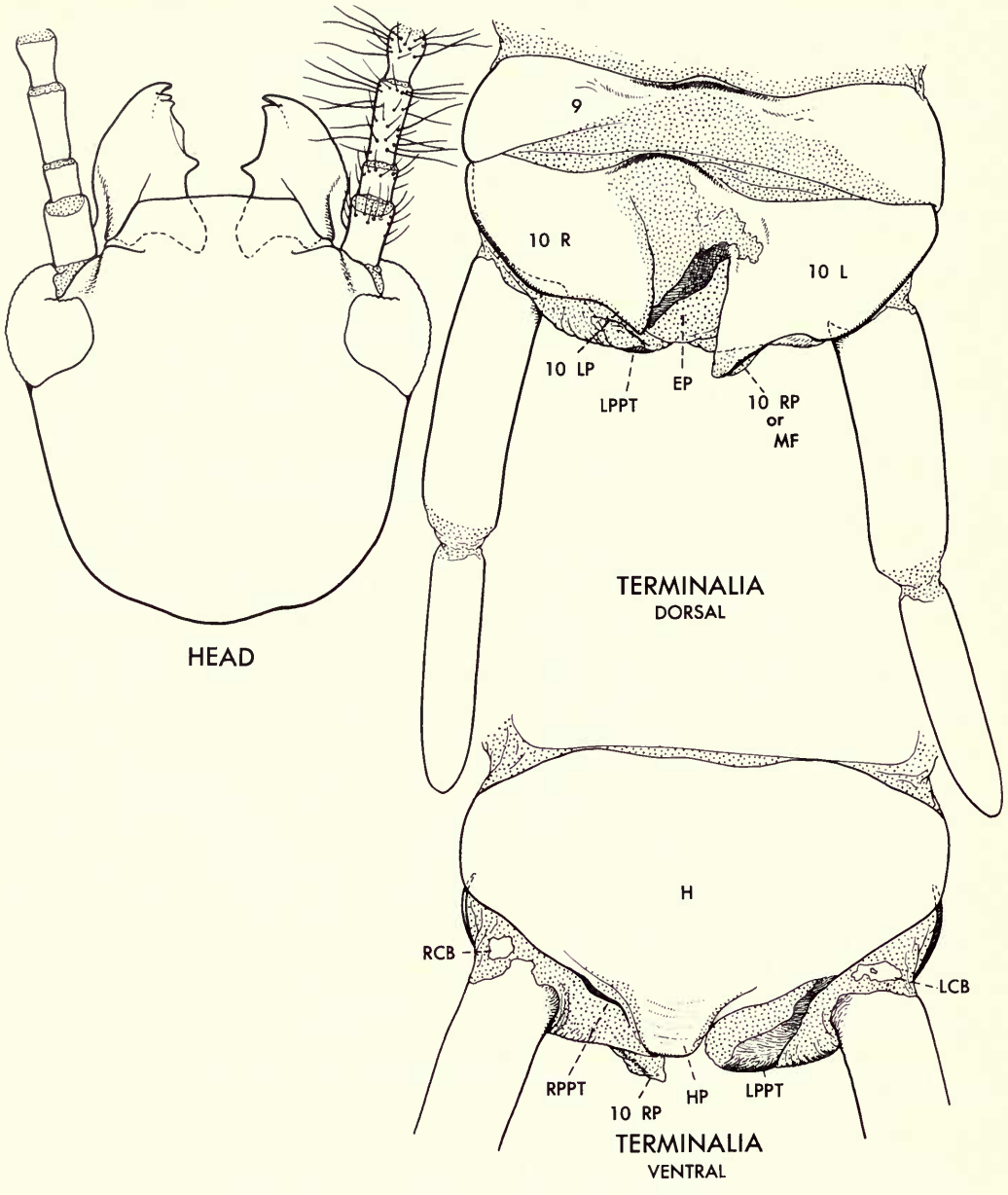


FIGURE 11. *Chromatoclothoda nigricauda* Ross, new species. Head and terminalia of holotype. For an explanation of symbols see page 10.

DESCRIPTION.—Appearance: Small for family, about size and appearance of *Oligotoma saundersii*; winged; thorax and legs largely yellowish; head, abdomen, and wings dark brown; cerci entirely brown; antennae white-tipped. Color details (in alcohol): Cranium mahogany-brown with faint, paler pattern; golden-brown ventrally. Eyes dark lavender with golden margins. Antennal segments I–XIII dark brown, basal segment not much darker than sub-basals; segment XIV basally brown, apical two-thirds pale amber; segments XV–XVIII white (segmentation complete), vestiture white. Mandibles dark mahogany-brown to amber-brown; submentum

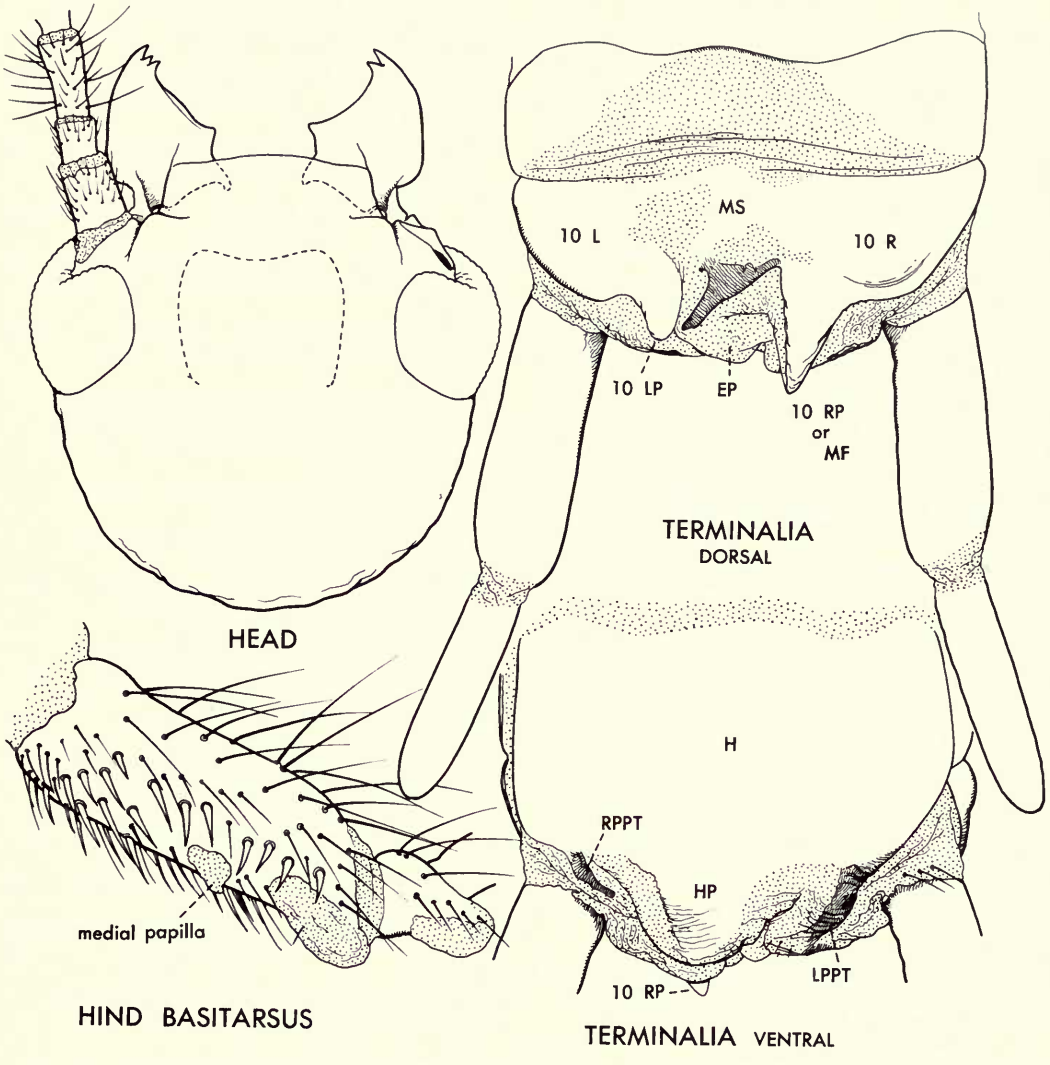


FIGURE 12. *Chromatoclothoda nana* Ross, new species. Head and terminalia of holotype. For an explanation of symbols see page 10.

golden-brown, concolorous with gula; palpi dark brown. Thorax basically pale, straw-yellow with piceous setae, membranes cream-white; lateral and anterior margins of pronotum and dorsal fold of cervix tinged with bright orange; margins and sutures of pterothorax chestnut-brown, caudal region of metathorax strongly tinged with rust-orange. Coxae and trochanters of all legs cream-yellow, femora blending to golden-brown, all tibiae and tarsi chestnut-brown. Wing pigmentation as in *C. elegantula* but lighter brown, with hyaline intervals more sharply defined. All abdominal sclerites, including those of terminalia as well as all cercus segments, red-brown; all abdominal membranes red-purple. Dimensions (on slide): Body length 8.5 mm; fore wing length 6.0 mm, breadth 1.4 mm.

Important anatomical characters (Fig. 12): Cranium circular in outline with irregular caudal margins. Eyes rather large. Antennal segments elongate; setae erect and wavy. Mandibles oligotomoid, dorsoventrally thin; apical teeth sharply

defined, acute. Submentum flat, smooth, longer than broad; sides and front edges inflexed; evenly, but not heavily, sclerotized. Wings with rather broad hyaline intervals. Hind basitarsi with few large plantar setae and small, medial, ventral papilla. Tenth abdominal tergite with basomedial area weakly and irregularly sclerotized; left process (10 LP) weak, rounded, thumblike; right process (10 RP) rather long, acutely triangulate, apex blunt. Epiproct sclerite prominent, relatively darkly pigmented, gradually broadened toward base. Lobe of ninth sternum (HP) medial; edges irregular; blending to membrane. Left paraproct (LPPT) attached basally to H, otherwise separated by wide membranous gap from HP, transversely striate, apically weak; right paraproct (RPPT) represented only by well-pigmented basal rudiment. Cerci equal, distal segments shorter than basals.

Female: No specimens.

PARATYPE.—One male with type data, CAS.

DISCUSSION.—*Chromatoclothoda nana,* the smallest, most apomorphic species of the family, is readily distinguished by its small size and head and terminalia characters, particularly the large epiproct and its basally broad sclerite. The form of the right tergal process and the development of the epiproct, with a tendency for a transverse membranous gap to intervene between these structures and the right hemitergite, constitute the first stage in evolution of the type of terminalia found in *Oligotoma, Oligembia,* and related genera.

HABITAT.—Debris-covered galleries in crevices of stump bark in field at edge of virgin forest.

ACKNOWLEDGMENTS

Fieldwork and laboratory studies were in part supported by grants from the National Science Foundation, John Simon Guggenheim Foundation, The Conservation Agency, and the National Geographic Society. The following individuals assisted in the field, or provided specimens for study: Dr. José Carvalho, Dr. St. von Kéler, Dyrce Lacombe, Clark E. Ross, and Dr. Evert I. Schlinger.

LITERATURE CITED

ARNAUD, P. H. 1963. *Perumyia embiaphaga,* a new genus and species of Neotropical Tachinidae (Diptera) parasitic on Embioptera. Am. Mus. Novit. 2143:1–8. 14 fig.

COCKERELL, T. D. A. 1908. Descriptions of Tertiary Insects II. Am. J. Sci. (4)25:227–232.

DAVIS, C. 1939. Taxonomic notes on the order Embioptera. IV. The genus *Clothoda* Enderlein. Proc. Linn. Soc. N.S.W. 64:373–380. 25 fig.

———. 1940*a*. Taxonomic notes on the order Embioptera. XX. The distribution and comparative morphology of the order Embioptera. Proc. Linn. Soc. N.S.W. 65:533–542. 4 fig.

———. 1940*b*. Family classification of the order Embioptera. Ann. Entomol. Soc. Am. 33:677–682.

———. 1942. Report on a collection of Embioptera from Trinidad and Guiana. Proc. R. Soc. Lond. B. Biol. Sci. 11:111–119. 15 fig.

DENIS, R. 1949. Ordre des Embioptères. Pp. 723–744 *in* Traité de Zoologie, Vol. 9, P. Grassé, ed. Masson et Cie, Paris. 14 fig.

ENDERLEIN, G. 1909. Die Klassification der Embiidinen, nebst morphologischen und physiologischen Bemerkungen, besonders uber das Spinnen derselben. Zool. Anz. (Leipzig) 35:166–191. 3 fig.

———. 1912. Embiidinen. Coll. Zool. Selys-Longchamps. fasc. 3:1–121. 76 fig.

FRIEDERICHS, K. 1906. Zur Biologie der Embiiden. Mitt. Zool. Mus. Berl. 3:213–239. 19 fig.

GERSTAECKER, A. 1888. Das Gemeinschaftsleben der Embiiden und Nahers zur Kenntnis der Arten. Mitt. naturw. Ver. Neuvorpom. und Rugen. 20:1–2.

KALTENBACH, A. 1968. Embiodea (Spinnfüsser). Pp. 1–29 *in* Handbuch der Zoologie IV. Band: Arthropoda—2. Hälfte: Insecta 2. Teil: Spezielles 8. 43 fig.

KERSHAW, J. C. 1914. Development of an embiid. J. R. Microsc. Soc. 1914:24–27. Pl. 3, 4.

KIRKPATRICK, T. W. 1957. Insect life in the tropics. Longmans, Green and Co. xiv + 311 pp., ill.

KRAUSS, H. A. 1899. Was ist *Condylopalama agilis* Sund.? Zool. Anz. (Leipzig) 22:147–148.

———. 1911. Monographie der Embien. Zoologica (Stuttg) 23:1–78. 7 fig., 5 pl.

MATSUDA, R. 1960. Morphology of the pleurosternal region of the pterothorax in insects. Ann. Entomol. Soc. Am. 53:712–731. 38 fig.

MC C. CALLAN, E. 1952. Embioptera of Trinidad with notes on their parasites. Trans. Ninth Int. Congr. Entomol. 1:483–489. 1 tab.

MELANDER, A. L. 1903. Notes on the structure and development of *Embia texana.* Biol. Bull. (Woods Hole) 4:99–118. 6 fig.

NAVÁS, L. 1918. Embiópteros (Ins.) de la América Meridional. Broteria, Zool. ser. 16:85–110. 6 fig.

ROSS, E. S. 1944. A revision of the Embioptera, or webspinners, of the New World. Proc. U.S. Nat. Mus. 94:401–504. 156 fig., 2 pl.

———. 1984. A synopsis of the Embiidina of the United States. Proc. Entomol. Soc. Wash. 86:82–93. 4 fig.

SAUSSURE, H. DE. 1896*a*. Two Embiidae from Trinidad. J. Trinidad Field Nat. Club. 2:292–294.

———. 1896*b*. Note sur la tribu des Embiens. Mitt. Schweiz. Entomol. Ges. 9:339–355. 1 pl.

TILLYARD, F. 1937. Kansas Permian insects, pt. 18: The order Embiaria. Am. J. Sci. (5) 33:241–251. 3 fig.

PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 3, pp. 35-82, 9 figs., 1 table February 5, 1988

A REVIEW OF THE SOUTHEASTERN PACIFIC *CORYPHAENOIDES* (SENSU LATO) (PISCES, GADIFORMES, MACROURIDAE)

By

Tomio Iwamoto

Department of Ichthyology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

and

Yu. I. Sazonov

Laboratory of Oceanic Ichthyofauna, P. P. Shirshov Institute of Oceanology, Academy of Sciences, USSR, 117218, Moscow, Krasikov St. 23, USSR

SAN FRANCISCO

PUBLISHED BY THE ACADEMY

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 3, pp. 35–82, 29 figs., 1 table. February 5, 1988

A REVIEW OF THE SOUTHEASTERN PACIFIC *CORYPHAENOIDES* (SENSU LATO) (PISCES, GADIFORMES, MACROURIDAE)

By

Tomio Iwamoto

Department of Ichthyology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

and

Yu. I. Sazonov

Laboratory of Oceanic Ichthyofauna, P. P. Shirshov Institute of Oceanology, Academy of Sciences, USSR, 117218, Moscow, Krasikov St. 23, USSR

ABSTRACT: The grenadier genus *Coryphaenoides* is represented by 14 species in the southeastern Pacific, including two new ones: *C. oreinos* (5 specimens from off Mexico) is closest related to *M. bucephalus*, differing primarily in having a more rounded and naked snout, different squamation, and broader head; *C. myersi* (known only from the holotype taken in the Galapagos) is closely related to *C. capito* and *C. boops*, but differs in having a shorter, stubbier snout and more pelvic rays. Small individuals of these two last species were difficult to distinguish; Garman in fact included two specimens of *C. capito* in the type series of *C. boops*. *Macrurus latinasutus* Garman, 1899, and *M. liraticeps* Garman, 1899, are considered synonyms of *M. anguliceps* Garman, 1899. *Macrurus leucophaeus* Garman, 1899, is questionably placed in the synonymy of *C. capito*. Other species treated are: *C. ariommus, C. armatus, C. bucephalus, C. bulbiceps, C. carminifer, C. delsolari, C. fernandezianus* (no new material), *C. filicauda*, and *C. paradoxus*. Provisional diagnoses are provided for subgenera *Chalinura, Coryphaenoides, Lionurus*, and *Nematonurus*, and a preliminary hypothetical phylogeny of macrourids with six branchiostegal rays is presented.

CONTENTS

Acknowledgments 36
Introduction 36
Materials and Methods 36
Genus *Coryphaenoides* Gunnerus, 1765 38
List of *Coryphaenoides* Species 40
Key to Adults of *Coryphaenoides* Species from the Southeastern Pacific 42
Subgenus *Coryphaenoides* Gunnerus, 1765 45
C. anguliceps (Garman, 1899) 45
C. ariommus Gilbert and Thompson, 1916 50
C. boops (Garman, 1899) 53
C. bucephalus (Garman, 1899) 57
C. bulbiceps (Garman, 1899) 59
C. capito (Garman, 1899) 62
C. carminifer (Garman, 1899) 64
C. delsolari Chirichigno and Iwamoto, 1977 66
C. oreinos Iwamoto and Sazonov, n. sp. 68

C. myersi Iwamoto and Sazonov, n. sp. 71
C. paradoxus (Smith and Radcliffe, 1912) 72
Subgenus *Nematonurus* Günther, 1887 75
C. armatus (Hector, 1875) 75
Subgenus *Chalinura* Goode and Bean, 1883 76
C. fernandezianus (Günther, 1878) 77
Subgenus *Lionurus* Günther, 1887 77
C. filicauda Günther, 1878 77
Literature Cited 79

Acknowledgments

We thank the many persons who helped in various ways in the production of this work. Our apologies to any we have inadvertently failed to list. Our special thanks to N. V. Parin (IOAN) who initiated this collaborative effort and provided valuable specimens. We also acknowledge the advice and assistance provided by M. E. Anderson (CAS), T. Arai (Tokyo), D. M. Cohen (LACM), W. N. Eschmeyer (CAS), O. Okamura (BSKU), Y. N. Shcherbachev (IOAN), K. J. Sulak (ARC), and I. A. Verighina (MMSU). The following provided loans and/or courtesies during visits to their respective institutions: A. Wheeler (BMNH); T. Sato and K. Wakabayashi (FSFL); C. E. Dawson (GCRL); N. Chirichigno (IMARPE); D. M. Cohen, R. J. Lavenberg, J. A. Seigel, and staff (LACM); K. E. Hartell, K. F. Liem, and staff (MCZ); R. H. Rosenblatt and staff (SIO); R. H. Gibbs, V. G. Springer, J. R. Gomon, and S. Jewett (USNM). Technical assistance was provided by M. E. Anderson, D. Catania, L. J. Dempster, and P. Sonoda. D. M. Cohen (LACM), D. L. Stein (OSUO), and N. R. Merrett (IOS) greatly improved the manuscript through their critical reviews. S. Middleton and J. Patton made photographs of specimens and drawings; K. P. Smith drew the fine illustration (Fig. 13) of *C. boops*.

Introduction

This paper continues a series treating the Macrouridae of the eastern Pacific begun with Iwamoto and Stein's (1974) review of northeastern Pacific grenadiers followed by articles by Chirichigno and Iwamoto (1977), Hubbs and Iwamoto (1977), and Iwamoto (1978, 1979).

The genus *Coryphaenoides* is represented by 20 species in the eastern Pacific and is well represented in several other parts of the world where sufficient deep-water sampling has shown them to be present. Iwamoto and Stein (1974) reported on seven *Coryphaenoides* species (excluding *Albatrossia pectoralis* (Gilbert, 1892), included in *Coryphaenoides*) from the boreal eastern North Pacific. In this paper we treat the 13 remaining eastern Pacific members of the genus, including two new species. We report again on the wide-ranging *C. armatus* Hector, 1875, which was treated by Iwamoto and Stein (1974), but for which additional pertinent information has been recently published.

Materials and Methods

Most of the specimens used in compiling this review are from collections of the California Academy of Sciences (CAS and CAS-SU), Museum of Comparative Zoology, Harvard (MCZ), and the National Museum of Natural History (USNM), but important additions were obtained from the recent Soviet collections housed at the Zoological Museum of Moscow State University (MMSU), the P. P. Shirshov Institute of Oceanology, Moscow (IOAN), and the collections of the Instituto del Mar, Callao, Peru (IMARPE), the Los Angeles County Museum of Natural History (LACM), and Scripps Institution of Oceanography (SIO). Abbreviations for institutions follow the Standard Symbolic Code for Institutional Research Collections in Herpetology and Ichthyology (Leviton et al. 1985).

Garman's (1899) valuable work, in which he described 6 of the 14 species here treated, was based on an ALBATROSS collection made during a cruise to the eastern tropical Pacific in 1891. Garman apparently did not examine collections from an 1888 ALBATROSS cruise around the tip of South America, north along the Pacific coasts of South and Central America, and out to the Galapagos, although many of the species he described were collected during that voyage. Gilbert and Thompson (1916) later reported on that portion of the collection procured between Montevideo, Uruguay, and Tome, Chile, but it was not until recently that some of the macrourids collected from low-latitude waters were treated (see Iwamoto 1978, 1979). Most material from that 1888 voyage was poorly preserved, and the macrourid specimens have deteriorated badly.

A subsequent ALBATROSS cruise to the trop-

ical eastern Pacific in 1904 resulted in the collection of additional macrourid specimens, some of which are here reported (others were treated by Iwamoto 1979). Carl L. Hubbs told one of us (Iwamoto, pers. comm., ca. 1976) of having examined the 1888 and 1904 collections in preparing with C. H. Gilbert their two monumental works on macrourids (Gilbert and Hubbs 1916, 1920), but other commitments diverted him from completing his studies on them.

Most recent CAS macrourids used here were collected by the ANTON BRUUN in 1966 during the Southeastern Pacific Biological Oceanography Program (SEPBOP), and by Margaret G. Bradbury in 1968 on a cruise of the former Stanford University vessel TE VEGA. The LACM macrourids utilized were chiefly procured by the VELERO IV and other vessels through the efforts of Curator Robert J. Lavenberg and his colleagues at the LACM. The LACM's extensive ELTANIN collections from the Southern Ocean were used for comparison of some species and for the description of *Coryphaenoides filicauda*. The IOAN macrourids are from recent Soviet fisheries surveys in the southeastern Pacific, including the Nazca and Sala-y-Gomez ridges off Peru and Chile (see Parin et al. 1980). The entire macrourid fauna of these ridges will be reported by us in a separate publication.

Methods for making counts and measurements generally follow Gilbert and Hubbs (1916) and Iwamoto (1970). Definitions and abbreviations are explained below. In the Diagnosis sections, the numbers within parentheses refer to exceptional counts and measurements, at least in our material.

Counts

1D. and 2D.—Counts of the first and second dorsal fin rays. The Roman numerals "II" refer to the two spinous rays of the first dorsal, the first ray is usually rudimentary and closely appressed to the elongated and serrated second spinous ray; the Arabic numbers that follow refer to the segmented rays.

1P.—Pectoral fin ray count. The lowercase "i" refers to the rudimentary or short uppermost ray that is frequently closely appressed to the larger second ray.

V.—Pelvic fin ray count.

A.—Anal fin ray count.

GR-1 and GR-2—Gill raker counts of the first and second arches. Both inner and outer series are given. In the following, "(2–5) / (1–2) + (0–1) + (6–7) [7–9 total]," the outer and inner series are separated by a slash mark; the first figures within parentheses indicate the presence of 2–5 rakers on the outer series; in the inner series there are 1–2 rakers on the dorsal arm, 0 or 1 raker at the angle, 6–7 rakers on the lower arm, and 7–9 total rakers. When it could not be determined if a raker at the angle resided on the upper or lower arm, it was included in the lower-arm count.

Scales 1D., 2D., mid-1D., lat.l.—Scale row counts, respectively, below the origin of the first dorsal fin, second dorsal fin, mid-base of first dorsal fin, and lateral line scales counted from the anterior origin over a distance equal to the predorsal length. Lateral line scales are not included in the first three counts, and half-scale (0.5) counts are given when the uppermost scale is considerably smaller than others of the series.

Precaud. vert.—Precaudal vertebrae count.

Caeca—Pyloric caeca count; includes all distal tips.

Measurements

Measurements of fins and trunk parts are often imprecise because of distortion caused by preservation and are rounded to the nearest 1.0 mm. Head parts are measured to the nearest 0.1 mm.

Postrostral—Distance from anteriormost edge of orbit to posteriormost extent of operculum.

TL—Total length, snout tip to posteriormost extent of tail. A plus sign (+) indicates that a portion of the tail tip was missing or that a pseudocaudal was present.

HL—Head length, taken from snout tip to upper posterior angle of opercle.

Snout—Snout length, taken from tip of snout to anterior edge of orbit.

Preoral—Median ventral measurement from snout tip to (but not including) upper lip.

Internasal—Least distance between supranarial ridges.

Interorbital—Least distance between bony orbits.

Orbit—Greatest orbital diameter, often oblique.

Suborbital—Least width of suborbital space.

Postorbital—Horizontal measurement along

midorbital axis from posterior rim of orbit to posteriormost extent of operculum.

Orbit–preop.—Oblique measurement from posteroventral edge of orbit to posteroventral angle of preoperculum.

Upper jaw—Length from anteriormost tip of premaxilla to posterior edge of maxilla.

Rictus—Length from symphysis of upper jaw to posteriormost extent of mouth opening.

Nostril—Greatest diameter of posterior nostril.

Barbel—Length from base (posterior insertion) to tip.

Gill slit—Greatest length of opening between gill cover and first gill arch.

Pre-D., pre-A., pre-V.—Predorsal, preanal, and prepelvic lengths, taken from snout tip to origin of first dorsal, anal, and pelvic fins, respectively.

V.–A.—Measurement from base of outer pelvic ray to origin of anal fin.

Isth.–A.—Measurement from anterior end of scaled area of chest to origin of anal fin.

Body depth—Greatest body depth taken below origin of first dorsal fin.

1D.–2D.—Distance from posterior base of first dorsal to origin of second dorsal fin; the latter point often difficult to discern because of the rudimentary anteriormost rays.

1D., 1P., V.—Height of first dorsal, lengths of pectoral and pelvic fins, respectively.

Genus **Coryphaenoides** Gunnerus, 1765

Coryphaenoides Gunnerus, 1765 (type species *Coryphaenoides rupestris* Gunnerus, 1765, by monotypy).
(See Iwamoto and Stein [1974] for synonymy.)

Diagnosis.—Branchiostegal rays 6. Anus immediately in advance of anal fin or slightly anterior to it; no light organ. Barbel present. Dentition variable among species, from broad bands to 1 or 2 rows, but teeth never few and fanglike. Snout shape variable, from pointed to bluntly rounded, but never greatly produced beyond mouth. Suborbital ridge extends from lateral angle of snout to below hind edge of orbit; not connected to preopercular ridge. Second spinous ray of first dorsal fin usually slightly prolonged and serrated along leading edge, rarely completely smooth. Anterior rays of second dorsal fin never as well developed as opposite of anal fin. A distinct interspace between dorsal fins, usually more than half length base of first dorsal. Gill rakers tubercular to short and tablike (or spatulate); those of outer series on first arch often few and rudimentary. Precaudal vertebrae 11–16. Pyloric caeca simple, unbranched, stublike to long and slender; usually fewer than 20. Retia and gas glands 4–7 each. (Modified from Iwamoto and Stein [1974]. See also Okamura [1970*a*, *b*] for additional characters.)

Discussion and Relationships.—The species of *Coryphaenoides* are among the deepest-living members of the family, most being found deeper than about 500 m, with species of subgenera *Nematonurus, Chalinura,* and *Lionurus* generally found well below 2,000 m to as much as 6,160 m (the last figure reported by Horibe [1983] for specimens that are probably *C. yaquinae* from the North Pacific).

Coryphaenoides as here defined represents a diverse array of species whose interrelationships are poorly understood. Based on our ideas, we present a phylogeny in Figure 1. Though very tentative and not based on a rigorous evaluation of characters, it is presented to allow future workers to test our ideas. It will undoubtedly face much alteration when more synapomorphies are found to establish monophyletic groups. The subgenera and species groups have not been adequately established, accounting for the many unresolved nodes. We recognize that the use of as plastic a character as rete mirabile numbers may erroneously infer relationships that do not exist, but we have used it lacking anything better. Rete numbers in *Lepidorhynchus,* for example, may be as high as 9 (Marshall 1965), and in *Coelorinchus canus* they vary between 6 and 11, although most others of the genus have only 4 retia. It is difficult to reconcile in our minds that *Coelorinchus* and *Macrourus* are closer relatives of *Coryphaenoides* than are *Albatrossia, Hyomacrurus, Coryphaenoides serrulatus,* and *C. subserrulatus.* Yet using rete numbers forces this assumption as the most parsimonious.

We follow Iwamoto and Stein's (1974) use of the subgeneric categories *Coryphaenoides, Nematonurus, Lionurus,* and *Chalinura,* although others (Parr 1946; Nybelin 1957; Marshall 1973) feel they deserve full generic standing. From the diversity seen, it is apparent to us that other genera or subgenera will eventually be recognized, as species groups within the genus become better known and synapomorphies are identified. Two genera have recently been removed from

Coryphaenoides: *Albatrossia* Jordan and Evermann, 1898 (because of its peculiar otolith, squamation, two retia, and reduced swim bladder) and *Hyomacrurus* Gilbert and Hubbs, 1920 (two retia, anus far removed from anal fin). Other candidates for separate recognition are *Macrurus longifilis* Günther, 1877 (in *Bogoslovia*); *Coryphaenoides serrulatus* Günther, 1878, and *C. subserrulatus* Makushok, 1976; and *Macrurus zaniophorus* Vaillant, 1888 (and its several close relatives including *Macrourus carminifer, M. boops, M. capito,* and *Coryphaenoides paramarshalli,* among others). The type species of *Coryphaenoides, C. rupestris,* differs so much from most members of the genus as here used that it too is a distinct candidate for separation from the group. (The genus name *Hemimacrurus* Fraser-Brunner, 1935 [type species *Macrurus acrolepis* Bean, 1884] is available for the remaining species in the event that should happen.)

We recognize approximately 61 species (see List) of *Coryphaenoides* (sensu lato). Seven other genera share the derived feature of six branchiostegal rays: *Albatrossia, Coelorinchus, Cynomacrurus, Hyomacrurus, Lepidorhynchus, Macrourus,* and *Odontomacrurus.* Of these, the monotypic *Odontomacrurus* (*murrayi* Norman, 1939) and *Cynomacrurus* (*piriei* Dollo, 1909) are so bizarre, with their bathypelagic habit, terminal mouth, no projecting rostrum, and fanglike teeth, that their relationship with the remaining genera must be very distant. Similarly, *Lepidorhynchus* (*denticulatus* Richardson, 1846) is notably different in having a luminescent organ with ventral striae, a character shared only with the seven-branchiostegal-rayed *Hymenocephalus* and a few distant gadiforms and higher teleosts. *Coelorinchus* and *Macrourus* represent a well-defined monophyletic line characterized by the sharply pointed and heavily scuted posteroventral angle of the preopercular ridge; strong, modified scutelike scales on head ridges; and absence of gill rakers on the outer side of the first gill arch. All members of *Coelorinchus* have a ventral light organ, some highly developed. A small structure has been observed in the body wall immediately anterior to the anus in *Macrourus*; it may very well represent a rudimentary or primitive state of light organ, which, if so, would be another synapomorphy for this line.

The number of known species within *Coryphaenoides* will undoubtedly increase with ad-

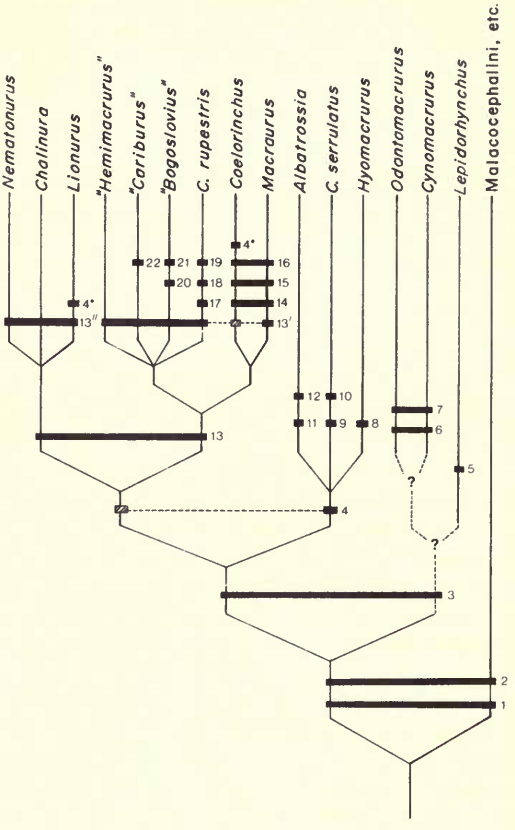


FIGURE 1. Tentative phylogeny of macrourines with six branchiostegal rays. Apomorphic character states indicated by numerals as follows [plesiomorphic states in square brackets]: (1) A. better developed than 2D. [2D. larger than A.]; (2) dorsal fins separated by a distinct gap [no gap]; (3) branchiostegal rays 6 [7]; (4) serrated 1D. spinous ray [smooth]; (5) ventral striae [none]; (6) reductions related to bathypelagic habit [none]; (7) fanglike teeth [small teeth]; (8) anus remote from A. [immediately in advance of A.]; (9) lanceolate scale spinules [conical]; (10) outer gill rakers on first arch tablike or spatulate [lathlike or tubercular]; (11) swim bladder reduced [normally developed]; (12) saccular otolith elongated [oval]; (13) retia numbers more than 2 [2]; (13′) retia 4 [2]; (13″) retia 5–7 [2]; (14) angle of preopercle ridge sharp, reinforced with stout scutelike scales [rounded, scales normal]; (15) outer gill rakers on first arch absent [present]; (16) light organ present [absent]; (17) inflated head [normal]; (18) high number of gill rakers, more than 17 [fewer than 17]; (19) scale patches on gular membrane [absent]; (20) reduced scale size [normal]; (21) premaxillary teeth in 2 widely separated rows [in bands or closely spaced rows]; (22) jaws short, with mouth opening restricted posterolaterally by lip folds [jaws moderate to large, mouth opening unrestricted]. Asterisk (*) indicates plesiomorphic condition found in some species within lineage; hatched boxes indicate some species within lineage may have either a more derived or a plesiomorphic condition.

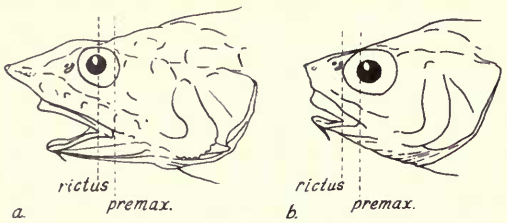


FIGURE 2. Diagrammatic illustrations of two species of grenadiers showing posterior extent of mouth opening (the rictus) and upper jaw (more specifically, the maxillary bone): (a) upper jaw extends to below posterior ⅓ of orbits, rictus to vertical through midorbit; (b) upper jaw ends short of level of midorbit, rictus extends to vertical through anterior ⅓ of orbit.

ditional collecting in the poorly known waters of the mid-Pacific, the western South Pacific, the Indo-Australian region, and the entire Indian Ocean. We think that relatively few currently recognized species of the genus will be synonymized as almost all are well defined and most appear to be confined to broadly restricted zoogeographical areas. Notable exceptions in their distributions are *Coryphaenoides armatus, C. leptolepis* Günther, 1887, and perhaps, *C. paradoxus* (Smith and Radcliffe, 1912) (if *C. macrocephalus* Maul, 1951, is a synonym). The first species has been thought to have a cosmopolitan distribution; Wilson and Waples (1983, 1984) have recently added significant insights into its zoogeography and taxonomy. They reported that *C. armatus* is generally confined in the Pacific to continental rise and slope areas between 2,000 and 4,300 m and is replaced in deeper waters by *C. yaquinae* Iwamoto and Stein, 1974. They recognized the North Pacific population as a distinct subspecies, *C. armatus variabilis*; populations from other areas represent the subspecies *C. a. armatus*. A few of the southernmost species of the genus, such as *C. subserrulatus* Makushok, 1976, *C. rudis* Günther, 1877, *C. filicauda* (Günther, 1878), and members of the subgenus *Nematonurus* are found in two or more ocean basins, but this is not surprising in that there is little to restrict their distributions in high-latitude southern waters. The apparent disjunction in the distribution of *C. rudis* between the western Indian Ocean and New Zealand is probably attributable to inadequate collecting off Australia and in the eastern Indian Ocean.

The *Coryphaenoides* species in this report are known for the most part only from adults and large juveniles. Collections of macrourid eggs, larvae, and prejuveniles remain scarce and unrepresentative of the diversity of this group. Mead et al. (1964) and Marshall (1965) summarized much of what was known to that time about reproductive and early stages of macrourid life. Recently, Merrett (1978), Stein (1980), and Stein and Pearcy (1982) reported on larval and prejuvenile stages of several species of *Coryphaenoides,* and Fahay and Markle (1985) provided a comprehensive summary of the little known about macrourid early life history. Much remains to be learned about the early life history of macrourids in general.

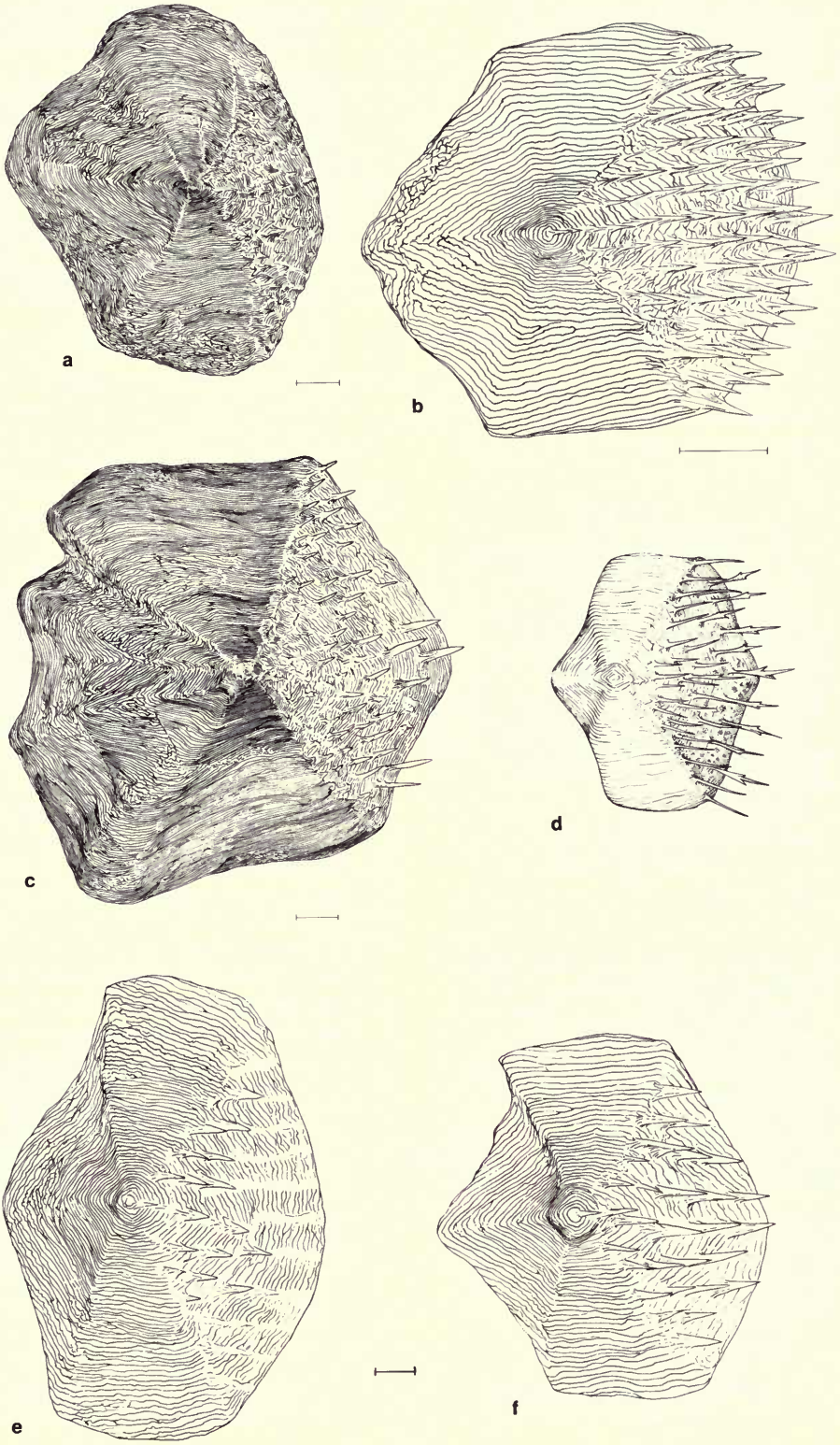
LIST OF *CORYPHAENOIDES* SPECIES
(Southeastern Pacific species indicated by an asterisk*)

Subgenus *Coryphaenoides* Gunnerus, 1765

1. *C. acrolepis* (Bean, 1884)
2. *C. aequatoris* (Smith and Radcliffe, 1912)
3. *C. alateralis* Marshall and Iwamoto, 1973
4. *C. altipinnis* Günther, 1877
5. *C. anguliceps* (Garman, 1899)*
6. *C. ariommus* Gilbert and Thompson, 1916*
7. *C. asper* Günther, 1877
8. *C. asprellus* (Smith and Radcliffe, 1912)
9. *C. boops* (Garman, 1899)*
10. *C. bucephalus* (Garman, 1899)*
11. *C. bulbiceps* (Garman, 1899)*
12. *C. camurus* (Smith and Radcliffe, 1912)
13. *C. capito* (Garman, 1899)*
14. *C. carminifer* (Garman, 1899)*
15. *C. cinereus* (Gilbert, 1895)
16. *C. delsolari* Chirichigno and Iwamoto, 1977*
17. *C. dubius* (Smith and Radcliffe, 1912)
18. *C. filamentosus* Okamura, 1970
19. *C. filifer* (Gilbert, 1895)
20. *C. guentheri* (Vaillant, 1888)
21. *C. hextii* (Alcock, 1890b)
22. *C. hoskynii* (Alcock, 1890a)

→

FIGURE 3. Body scales of *Coryphaenoides* spp. taken from region below interspace of dorsal fins, second to fourth row down: (a) *C. bulbiceps*; (b) *C. carminifer*; (c) *C. paradoxus*; (d) *C. delsolari* (from Chirichigno and Iwamoto 1977, fig. 2); (e, f) *C. oreinos*. Scale bars equal 1 mm.


a
b
c
d
e
f

23. *C. longicirrhus* Gilbert, 1905
24. *C. longifilis* (Günther, 1887)
25. *C. macrocephalus* (Maul, 1951)
26. *C. macrolophus* (Alcock, 1889)
27. *C. marginatus* Steindachner and Döderlein, 1887
28. *C. marshalli* Iwamoto, 1970
29. *C. mexicanus* (Parr, 1946)
30. *C. microps* (Smith and Radcliffe, 1912)
31. *C. myersi* Iwamoto and Sazonov, n. sp.*
32. *C. nasutus* Günther, 1877
33. *C. oreinos* Iwamoto and Sazonov, n. sp.*
34. *C. orthogrammus* (Smith and Radcliffe, 1912)
35. *C. paradoxus* (Smith and Radcliffe, 1912)*
36. *C. paramarshalli* Merrett, 1983
37. *C. rudis* Günther, 1878
38. *C. rupestris* Gunnerus, 1765
39. *C. semiscaber* Gilbert and Hubbs, 1920
40. *C. serrulatus* Günther, 1878
41. *C. sibogae* Weber and de Beaufort, 1929
42. *C. subserrulatus* Makushok, 1976
43. *C. thelestomus* Maul, 1951
44. *C. tydemani* (Weber, 1913)
45. *C. woodmasoni* Alcock, 1890b
46. *C. zaniophorus* (Vaillant, 1888)

Subgenus *Nematonurus* Günther, 1887
47. *C. armatus* (Hector, 1875)*
48. *C. ferrieri* (Regan, 1913)
49. *C. lecointei* (Dollo, 1900)
50. *C. yaquinae* Iwamoto and Stein, 1974
51. *C. affinis* (Günther, 1878)

Subgenus *Chalinura* Goode and Bean, 1883
52. *C. brevibarbis* (Goode and Bean, 1896)
53. *C. fernandezianus* (Günther, 1887)*
54. *C. leptolepis* Günther, 1877
55. *C. liocephalus* (Günther, 1887)
56. *C. mediterranea* (Giglioli, 1893)
57. *C. murrayi* Günther, 1878
58. *C. profundicola* (Nybelin, 1957)
59. *C. striatura* Barnard, 1925

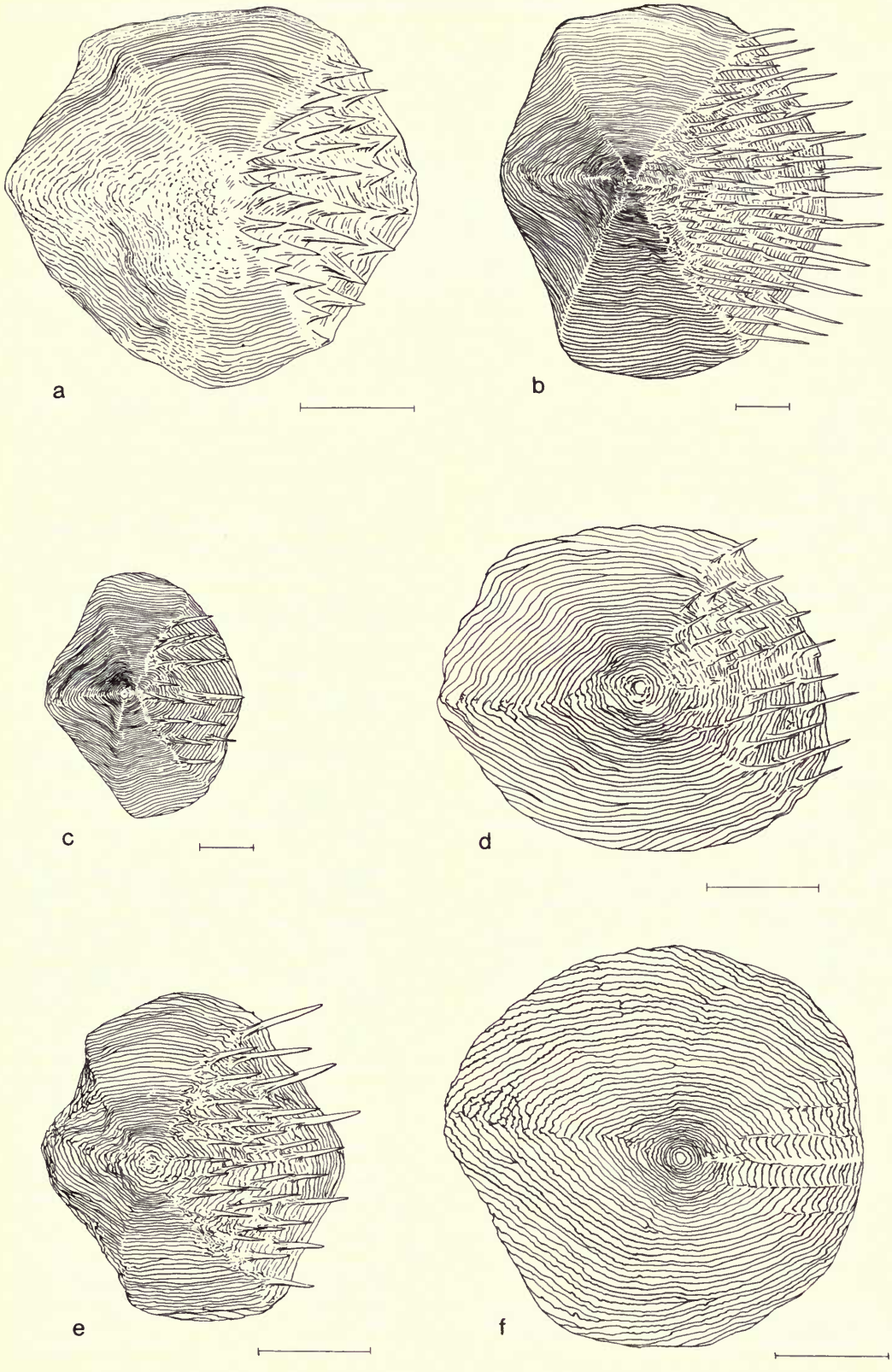
Subgenus *Lionurus* Günther, 1887
60. *C. carapinus* (Goode and Bean, 1883)
61. *C. filicauda* Günther, 1887*

Key to Adults of *Coryphaenoides* Species from the Southeastern Pacific

1a. Upper jaw extends to or beyond posterior ⅓ of orbits, length 35–45% HL; rictus extends to or beyond vertical through midorbit (Fig. 2a) 2
1b. Upper jaw ends at or short of level of midorbit, length usually 36% HL or less; rictus extends to or short of vertical through anterior ⅓ of orbit (Fig. 2b) 9
2a. Underside of snout fully scaled (ventral edge may be narrowly naked) 3
2b. Underside of snout naked 5
3a. V. 8 (rarely 9). Premaxillary teeth all small, in 1 row ..... *C. bulbiceps* (p. 59)
3b. V. 9–11. Premaxillary teeth in bands, with an enlarged outer series 4
4a. Orbit about 17% HL; barbel about equal to or greater than suborbital width; distance isthmus to A. equal to or more than HL. Body scales densely covered with short, fine, needlelike spinules (Fig. 3c) ..... *C. paradoxus* (p. 72)
4b. Orbit 23–34% HL; barbel length much less than suborbital width; distance isthmus to A. less than HL. Body scales with tridentate spinules (Fig. 3d) in specimens greater than 50 mm HL ..... *C. delsolari* (p. 66)
5a. Premaxillary teeth in 1 or 2 distinct rows ..... *C. armatus* (p. 75)
5b. Premaxillary teeth in bands 6
6a. Snout low, pointed, produced well beyond mouth. Mandibular teeth in narrow tapered band. 1D. spine smooth except for a few low denticulations distally. Spinulations on scales weak or absent, the few dispersed along 1–3 low ridges ..... *C. filicauda* (p. 77)
6b. Snout high, blunt, little produced beyond mouth. Mandibular teeth in 1 or 2 rows. Denticulations along entire leading edge of 1D. spine. Spinulations on scales well developed, in several parallel rows (Fig. 4c) 7
7a. Barbel 17–23% HL. Snout narrow, bluntly pointed. Outer premaxillary teeth notably large ..... *C. bucephalus* (p. 57)

→

Figure 4. Body scales of *Coryphaenoides* spp. taken from region below interspace of dorsal fins, second to fourth row down: (a) *C. ariommus*; (b) *C. boops*; (c) *C. bucephalus*; (d) *C. capito*; (e) *C. myersi*; (f) *C. anguliceps*. Scale bars equal 1 mm.


a
b
c
d
e
f

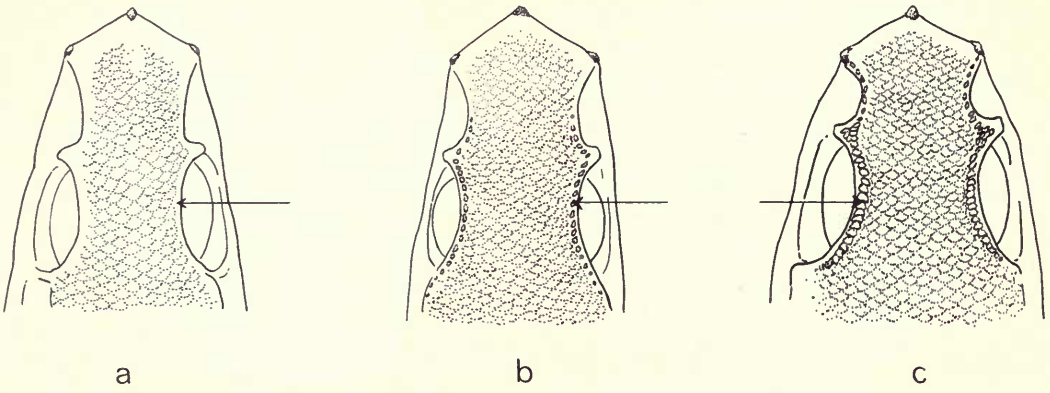


FIGURE 5. Squamation over dorsal surfaces of snout and interorbital region in (a) *C. anguliceps* (CAS 55832, 111 mm HL); (b) *C. ariommus* from off Peru (CAS 55835, 55.7 mm HL); and (c) *C. ariommus* from off Chile (CAS 55833, 82.5 m HL). Note larger scales over interorbital and absence of coarse scales along dorsal rim of orbit in *C. anguliceps.*

7b. Barbel 8–11% HL. Snout broad, rounded. Outer premaxillary teeth moderate in size 8

8a. Orbits 4–5 in HL. Mandibular teeth in narrow band 2–5 teeth wide ..... *C. oreinos*[1] (p. 68)

8b. Orbits 5.5 in HL. Mandibular teeth in single row ..... *C. fernandezianus* (p. 77)

9a. Barbel thick, stout, 14–23% HL; underside of snout scaled *C. carminifer* (p. 64)

9b. Barbel moderately thick to relatively thin and small, usually 11% HL or less; underside of snout mostly or entirely naked 10

10a. Body scales coarsely spinulated, adherent, those of suborbital shelf strongly adherent, in 2 or more rows and forming a distinct scaled edge to ventral rim of orbits. Snout low, scarcely protruding, preoral length less than 13% HL, 2.5–4 or more into greatest orbit diameter (which is 29–35% HL) 11

10b. Body scales thin and highly deciduous or heavily spinulated and moderately adherent; suborbital shelf mostly naked or with small scales in 1 or 2 rows that do not cover most of shelf and do not form a scaled ventral orbital edge. Snout variously produced and moderately high, preoral length 10–24% HL, 2.5 or less into orbit (which is 21–36% HL) 12

11a. V. 10, outer ray relatively thick and prolonged beyond 7th to 8th A. fin ray ..... *C. myersi* (p. 71)

11b. V. 7–8, outer ray thin, scarcely if at all reaching A. origin ..... *C. boops* (p. 53)

12a. Total gill rakers on inner series of first arch 11–14. Snout blunt, relatively short, 22–28% HL; suborbital narrow, 7–11% HL; interorbital narrow, 14–21% HL, 1.35–2.15 into orbit. Pyloric caeca short, stubby, 6–8 ..... *C. capito* (p. 62)

12b. Total inner gill rakers on first arch 7–10. Snout blunt or pointed, short to moderate in length, 26–35% HL; suborbital 11–16% HL; interorbital 17–29% HL, 0.95–1.59 into orbit. Pyloric caeca slender, 9–14 (in *C. ariommus* and *C. anguliceps,* unknown in *C. oreinos*) 13

13a. Snout high, bluntly rounded, length 25–28% HL. Mouth moderate 36–39% HL, rictus extends posteriad below anterior ⅓ orbit ..... *C. oreinos*[1] (p. 68)

13b. Snout low, pointed, length 28–35% HL. Mouth rather small, 26–35% HL, rictus extends to or slightly beyond anterior edge of orbits 14

14a. V. usually 9 (rarely 7, 8, or 10). Scales relatively adherent, coarsely spinulated (Fig. 4a), 12–15 rows across interorbital space (Fig. 5b, c); dorsal rim of orbits demarcated by a row of small, coarse,

[1] *Coryphaenoides oreinos* appears twice in the key (see also couplet 13a) in the event the jaw and rictus length characters of the first couplet are misinterpreted.

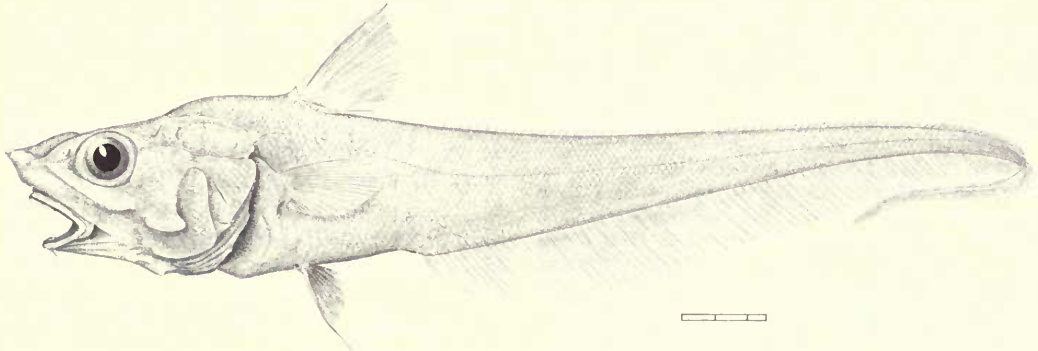


FIGURE 6. *Coryphaenoides anguliceps.* Composite drawing of CAS-SU 25227 (76 mm HL, 330+ mm TL) and CAS 55832 (76.3 mm HL, 352+ mm TL). Scale bar equals 25 mm.

adherent scales. Oral cavity blackish. Orbit 1.09–1.66 into distance orbit to angle of preopercle ... *C. ariommus* (p. 50)

14b. V. usually 8 (rarely 7 or 9). Scales highly deciduous, sparsely spinulated (Fig. 4f), 6–8 rows across interorbital space (Fig. 5a); no scales along dorsal rim of orbits. Oral cavity grayish. Orbit 1.60–2.22 into distance orbit to angle of preopercle. ..... *C. anguliceps* (p. 45)

Subgenus **Coryphaenoides** Gunnerus, 1765

DIAGNOSIS.—A subgenus of *Coryphaenoides* with 4 retia mirabilia. Origin of A. below or forward of 1D.–2D. interspace. Drumming muscles developed on swim bladder. Dentition pattern and size variable, usually in narrow to broad bands on premaxillary, with an enlarged outer series; mandibular teeth in 1–2 irregular rows or a band. Flesh generally firm; bones stout. Scales deciduous to adherent; spinules sometimes reduced or obsolescent. Snout acute to bluntly rounded; orbits small to large, diameter more than 20% HL in most species, usually about equal to or greater than interorbital width in small species (less than 40 cm TL). Upper jaw usually less than 45% HL; mouth opening greatly restricted in some species; upper jaw rarely extends beyond vertical through posterior ⅔ of orbit. Isthmus to A. distance in most species less than HL. Gill membranes usually broadly connected to isthmus with a narrow or no posterior free fold. Outer gill slit greatly restricted, less than 15% HL. GR usually fewer than 14 on inner series of first arch.

REMARKS.—The subgenus as here defined is a catchbasket for those species that do not readily fit into the other subgeneric categories. *Coryphaenoides serrulatus, C. subserrulatus,* and *C. longifilis* will not, in fact, fall into the circumscription of any of the subgenera here used—their placement will be considered in another paper. Much work still remains before the species groups are adequately sorted out, and the subgeneric diagnoses given here are highly provisional.

Coryphaenoides anguliceps (Garman, 1899)

(Figures 4f, 5a, 6–8, 11)

Macrurus anguliceps Garman, 1899:212–214, pl. G, fig. 1; pl. L; pl. 83, fig. 2 (type locality: Cocos Ridge between Panama and Galapagos; 5°56′N, 85°10.5′W; ALBATROSS sta. 3362 in 1,175 fm [2,149 m]; 26 Feb. 1891).

Coryphaenoides anguliceps: Gilbert and Hubbs 1916:144 (list).

Macrurus liraticeps Garman, 1899:196–197, pl. XLV, fig. 1–1b (type locality: Galapagos; 0°04′N, 90°24′30″W; ALBATROSS sta. 3407 in 885 fm [1,618 m]; 3 Apr. 1891). NEW SYNONYMY.

Coryphaenoides liraticeps: Gilbert and Hubbs 1916:144 (list).

Macrurus latinasutus Garman, 1899:214–215 (type locality: Gulf of California, ALBATROSS sta. 3431 in 1,820 m). NEW SYNONYMY.

Coryphaenoides latinasutus: Gilbert and Hubbs 1916:144 (list).

Lionurus latinasutus: Marshall 1973:596 (list).

Coryphaenoides anguliceps (?): Parin and Makushok 1973:180 (one adult, 340 mm TL; 2°S, 82°37′W, 2,150 m).

Macrouridae Gen. sp.: Parin and Makushok 1973:180 (juv., 63+ mm TL; 2°S, 82°37′W, 2,150 m).

MATERIAL EXAMINED.—Lectotype of *Macrurus anguliceps* Garman (here designated): MCZ 28558 (70.8 mm HL, 341 mm TL); ALBATROSS sta. 3362. Paralectotypes of *M. anguliceps*: MCZ 63000 (3: 58.5–69.8 HL, about 147–326 TL; all damaged; mixed, ALBATROSS sta. 3366, 3392, 3400).—MCZ 28562 (2: 64.3–70.2 HL, 307–354 TL); Gulf of California, 26°48′N, 110°45′20″W; 859 fm (1,571 m); ALBATROSS

sta. 3435; 22 Apr. 1891.—MCZ 28567 (1: 87 HL, 405+ TL) and MCZ 28588 (1: 58.4 HL); off Cocos I.; 5°30′N, 86°45′W; 1,067 fm (1,951 m); ALBATROSS sta. 3366; 27 Feb. 1891.—MCZ 28568 (1: 94 HL, 400+ TL) and USNM 57858 (2: 70.0–81.2 HL, 350+–340+ TL); off Cocos I.; 5°26′20″N, 86°55′W; 770 fm (1,408 m); ALBATROSS sta. 3371; 1 Mar. 1891.—MCZ 28563 (1: 74.0 HL, 334+ TL); Gulf of Panama; 7°06′15″N, 80°34′W; 695 fm (1,271 m); ALBATROSS sta. 3353; 23 Feb. 1891.—MCZ 28560 (4: 54.3–84.1 HL, 283+–412+ TL) and MCZ 28566 (1: 84.1 HL, 375+ TL); Gulf of Panama; 7°05′30″N, 79°40′W; 1,270 fm (2,323 m); ALBATROSS sta. 3392; 10 Mar. 1891.—MCZ 28565 (1: 75.8 HL, 365 TL); Gulf of Panama; 3°09′N, 82°08′W; 1,132 fm (2,070 m); ALBATROSS sta. 3376; 4 Mar. 1891.—MCZ 28559 (3: 72.2–76.6 HL, 337+–395+ TL); Cocos I.; 5°26′20″N, 86°55′W; 770 fm (1,408 m); ALBATROSS sta. 3371; 1 Mar. 1891.—MCZ 28569 (1: 85.3 HL, 400+ TL); Galapagos; 0°59′S, 88°58′30″W; 395 fm (722 m); ALBATROSS sta. 3400; 28 Mar. 1891.

Lectotype of *Macrurus liraticeps* (here designated): MCZ 28598 (112 HL, 500+ TL); Galapagos; ALBATROSS sta. 3407. Paralectotype: MCZ 63301 (1: 105 HL, 430 TL; same data as for lectotype).

Holotype of *Macrurus latinasutus*: MCZ 28557 (46.3 HL, 225+ TL); off mouth of Gulf of California; 23°59′N, 106°40′W; 995 fm (1,820 m); ALBATROSS sta. 3431; 20 Apr. 1891.

Other material.—MEXICO.—SIO 59-265 (13: 38.2–97.7 HL, 135+–422+ TL); Gulf of California, off Rio Glata; 23°40.5′N, 107°38.5′W, 747–757 fm (1,366–1,384 m); 11 May 1959.—SIO 65-233 (4: 67.7–91.4 HL, 328–401+ TL); SW of Cape region; 22°42.5′N, 110°21.0′W; 1,035–1,070 fm (1,893–1,957 m); HORIZON field no. MV-65-I-50; 28 June 1965.—LACM 31124-4 (4: 72.7–91.7 HL, 317+–416+ TL); Middle American Trench; 21°52′30″N, 106°46′36″W; 1,554 m; VELERO IV. sta. 13770; 21 Jan. 1970. COSTA RICA.—LACM 33588 (17: 67–94.0 HL, 285+–415 TL); 9°45′18″N, 85°52′24″W; 1,866 m; VELERO IV sta. 18932; 12–13 May 1973.—LACM 33643 (1: 67.4 HL, 330 TL); 8°36′N, 84°17′36″W; 2,240 m; VELERO 1V sta. 19037; 27 May 1973. COCOS ISLAND (96 km S of).—AMNH 7504 (3: 41.6–76.0 HL, 210+–340+ TL); ARCTURUS sta. 74; May 1925. ECUADOR.—USNM 135342 (1: 63.5 HL, 295+ TL) and USNM 148997 (1: 69.1 HL, 330+ TL); 1°03′N, 80°15′W; 741 fm (1,355 m); ALBATROSS sta. 2793, 3 Mar. 1888.—MMSU P-16520 (2: 17+–68 HL, 63+–340 TL); AKADEMIK KURCHATOV sta. 308 ("Proba" 253); 2°S, 82°37′W; 2,150 m. GALAPAGOS.—USNM 135343 (3: 46–101 HL, 188+–400+ TL); 0°24′S, 89°06′W; 812 fm (1,485 m); ALBATROSS sta. 2807; 4 Apr. 1888. PERU.—CAS 55832 (10 [of about 100]: 48.5–111 HL, 180+–466+ TL) and MMSU P-16514 (3 spec.); 4°10′S, 81°27′W; 1,815–1,860 m; ANTON BRUUN cr. 18B, sta. 766 (field no. LWK66-115); 9 Sep. 1966.

Diagnosis.—A species of *Coryphaenoides*, subgenus *Coryphaenoides*, with tiny chin barbel, about 3–4 into orbit. V. usually 8 (rarely 7 or 9). Mouth opening slightly restricted, rictus extends beyond vertical through anterior orbit margin, upper jaw extends to below midorbit. Small teeth in bands in both jaws. Snout pointed, protruding well beyond mouth. Body and head scales weak and highly deciduous; ventral and leading surfaces of snout naked; dorsal shelf region of suborbital mostly naked; suborbital ridge scales small, weak if present. Transverse scale rows across interorbital space 6–8. Oral cavity pale to grayish.

Counts and Measurements (83 spec.) (see also Table 1, and Fig. 6).—1D. II,8–10 (rarely 7); 1P. i18–i23 (usually i19–i21); V. 8 (rarely 7 or 9); 2D. about 100–118; A. 110–125; GR-1 (2–5) / (1–2) + (0–1) + (6–7) [7–9 total], GR-2 (1–2) + (0–1) + (5–7) [7–9 total] / (1–2) + (0–1) + (5–7) [7–9 total]; scales 1D. 6–8, 2D. 5.5–8.5, mid-1D. 3.5–5.5, lat.l. 39–46; caeca 9–14.

Total length 144+–460+ mm; HL 28.6–101 mm. The following in percent HL: postrostral 67.7–75.6; snout 27.8–34.0; preoral 15.7–22.9; internasal 16.5–22.5; interorbital 16.9–23.5; orbit 21.0–29.3; suborbital 11.7–15.0; postorbital 43.0–50.0; orbit–preop. 40.3–47.7; upper jaw 26.7–34.6; rictus 20.8–27.3; nostril 2.5–7.7; barbel 3.4–8.7; gill slit 5.3–8.7; pre-D. 107–117; pre-A. 135–174; pre-V. 104–125; V.–A. 34–57; isth.–A. 68–94; body depth 56–82; 1D.–2D. 15.5–48.7; 1D. 47–82; 1P. 36–57; V. 34–67.

Description.—Head large, fairly broad, greatest width about equal to postorbital length; length about 4.5–5.0 in TL. Nape prominently humped from behind orbits. Body long, slender, gradually tapered from level of first dorsal fin to end of tail. Orbits of moderate size, length 1.2–1.4 into snout length, about 4.2 in HL. Interorbital space narrow, slightly concave 1.1–1.4 into orbit. Snout pointed with a high median ridge; broad, width across lateral angles slightly more than orbit diameter, least width across supranarial ridges about equal to or more than interorbital space; snout tipped at terminal and lateral angles with stout, blunt scutes. Mouth relatively large; gape posterolaterally slightly restricted by lip folds; rictus extends to below anterior ¼ of orbits, end of maxillary to below midorbit, distance end of rictus to posterior end of maxillary about equal to barbel, which is very small, little longer than the small posterior nostril. Suborbital with a broad shelf and sharply angular (in cross section) longitudinal ridge which extends from tip of snout to anterior end of preopercle (the ridge not supported by bone between terminal and lateral angles of snout and for a short distance behind lateral angle). Preopercle broadly rounded, posterior margin inclined forward; preopercular ridge with a prominent lobelike prolongation at posteroventral angle. Interopercle almost entirely covered by preopercle, posterior edge barely exposed beyond preopercle margin.

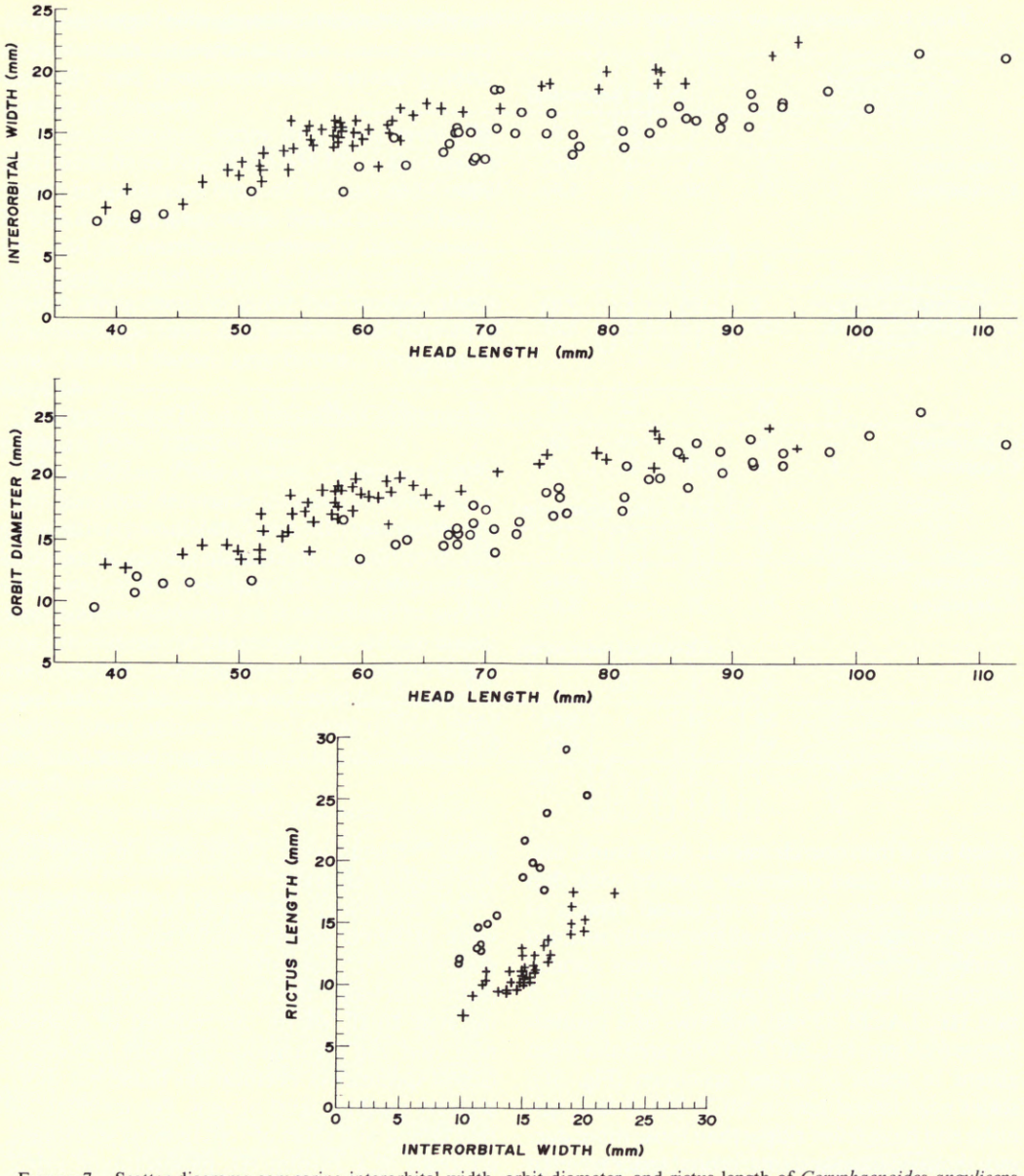


FIGURE 7. Scatter diagrams comparing interorbital width, orbit diameter, and rictus length of *Coryphaenoides anguliceps* (+) and *C. ariommus* (O).

Gill membranes broadly attached to isthmus, without a free posterior fold; opercular opening extends forward to below vertical arm of preopercular ridge. Gill slits, rakers, and filaments otherwise as described for *C. ariommus* (wh. see).

Scales highly deciduous, few remain in study material, although scale pockets prominently marked. Ventral surfaces and leading upper margin of snout naked except for terminal and lateral scutes. Dorsal surfaces of suborbital almost entirely naked, although a row of small, deeply embedded scales remain in the best-preserved specimens; lower surfaces of suborbital with a broad wedge of small scales. Nostril membranes and orbital margins naked. Anterior ⅓ or so of mandibular rami, all gill membranes, and ex-

TABLE 1. COMPARISONS OF FINRAY AND GILL RAKER COUNTS OF *CORYPHAENOIDES ARIOMMUS* AND *C. ANGULICEPS*.

	1D. rays (segmented)						
	7	8	9	10	$\bar{x}$	SD	*n*
C. ariommus	1	25	31	4	8.62	0.637	61
C. anguliceps	1	17	29	8	8.80	0.704	55

	V. rays						
	7	8	9	10	$\bar{x}$	SD	*n*
C. ariommus	—	3	106	6	9.02	0.280	115
C. anguliceps	3	106	4	—	8.01	0.250	113

	1P. rays											
	19	20	21	22	23	24	25	26	27	$\bar{x}$	SD	*n*
C. ariommus	—	4	15	49	28	5	2	1	1	22.28	1.11	105
C. anguliceps	6	18	33	31	7	1	—	—	—	21.14	1.09	97

	GR-1 (total inner series)						
	7	8	9	10	$\bar{x}$	SD	*n*
C. ariommus	—	2	27	31	9.48	0.567	60
C. anguliceps	1	29	27	—	8.47	0.537	57

	GR-2 (total inner series)						
	7	8	9	10	$\bar{x}$	SD	*n*
C. ariommus	2	24	31	3	8.58	0.645	60
C. anguliceps	3	48	6	—	8.05	0.397	57

posed tip of interopercle naked. All of trunk, tail, and most of head otherwise covered with thin deciduous scales. Scales over dorsal aspects of trunk covered with few small fine greatly reclined spinules arranged in low, more or less parallel longitudinal rows (8–12 rows in a specimen 67.5 mm HL, LACM 33588; 6–8 rows in a paralectotype 69.8 mm HL, MCZ 63300); spinules often absent in scales of largest specimen (Fig. 3f); scales near lateral line in MCZ 28558 lack spinules and have fewer ridges than those more dorsad; those on nape and interorbital space covered with short, erect, slender conical spinules. Terminal snout scute stout, somewhat conical with many rows of low stout spinules radiating from apex. In a 38-mm-HL specimen (SIO 59-265), scales below 1D. with 3–6 rows of slender, conical, sharp, much reclined spinules, the rows sharply defined, but because the spinules in a series overlap little, the rows do not appear ridge-like.

Teeth small, in bands in both jaws; the lower jaw band about 5–6 teeth wide, that of upper about 7–8 teeth wide. Outer series in upper jaw very slightly enlarged.

Fins moderately developed but rays generally weak. Height of second spinous ray of first dorsal about equal to postrostral length of head in most (somewhat longer in a few); serrations along leading edge small, sharp, but reduced or obsolete near base and filamentous tip (more reduced in largest specimens). Pectoral fins broad but short, scarcely reaching level of vent. Pelvics small, all rays falling well short of vent in most specimens, although in a 76-mm-HL paralectotype (MCZ 28559), outer ray extends to fifth anal ray; outer ray slightly prolonged into a hairfine tip. Second dorsal rudimentary throughout; anal fin well developed, but tips of rays broken off in all examined specimens.

Swim bladder large, fat-filled. Retia and gas gland bundle very small. Retia 4, long, slender, coiled; gas glands 4, peltate. Intestines complexly coiled, amount and complexity of loops variable among different individuals (see Fig. 8). Pyloric caeca long and slender, in an adherent mass, 9–

14 caeca, length of longest about equal to or longer than width interorbital space; caeca directed ventrally and posteroventrally around pyloric portion of stomach.

Color in alcohol varies from gray-brown in specimens from Peru (CAS 55832) to chocolate-brown in specimens from off Mexico and Cocos I., with descaled areas white. Naked areas of head, fins, and gill membranes generally dark brown. Oral lining grayish to dusky, lining of gill cavity grayish along shoulder girdle but blackish along branchiostegal rays. Gill arches and filaments pale. Mental barbel gray-brown. Peritoneum blackish.

DISTRIBUTION (Fig. 11).—Gulf of California to northern Peru, 722–2,418 m.

REMARKS AND COMPARISONS.—Garman (1899: 215) described *Macrurus latinasutus* from a single, relatively small (46.3 mm HL) specimen collected at the mouth of the Gulf of California. As with most of his descriptions, Garman gave no comparative diagnosis, so it is difficult to ascertain the reasons for his recognition of one taxon over another. Examination (by TI) of the holotype (MCZ 28557) showed nothing except a slightly lower pectoral fin ray count (i17 on both fins) that would suggest that it is other than conspecific with *C. anguliceps*.

The type specimens of *Macrurus liraticeps* (Garman) are large individuals of *C. anguliceps* that show pronounced reduction of serrations on the leading edge of the second spinous dorsal ray and reduction of spinulation on body scales. Garman (1889:197) was aware of the possibility that these features probably represented size-related changes, but he failed to connect the large specimens with the smaller type specimens of *Macrurus anguliceps* that he described on a subsequent page.

Specimens reported by Parin and Makushok (1973) as "*Coryphaenoides anguliceps* (?)" and "Gen. sp." were examined (by YIS) and confirmed as belonging to this species. The larger specimen (340 mm TL) has 9/9 pelvic fin rays, and two small scales remain at the upper margin of the orbit, but it otherwise agrees with the diagnosis of the species.

Relationships of *C. anguliceps* are closest to *C. ariommus*, and the ranges of the two overlap in northern Peru where they have been captured together (ANTON BRUNN sta. 766). The two species share a similar physiognomy, as well as

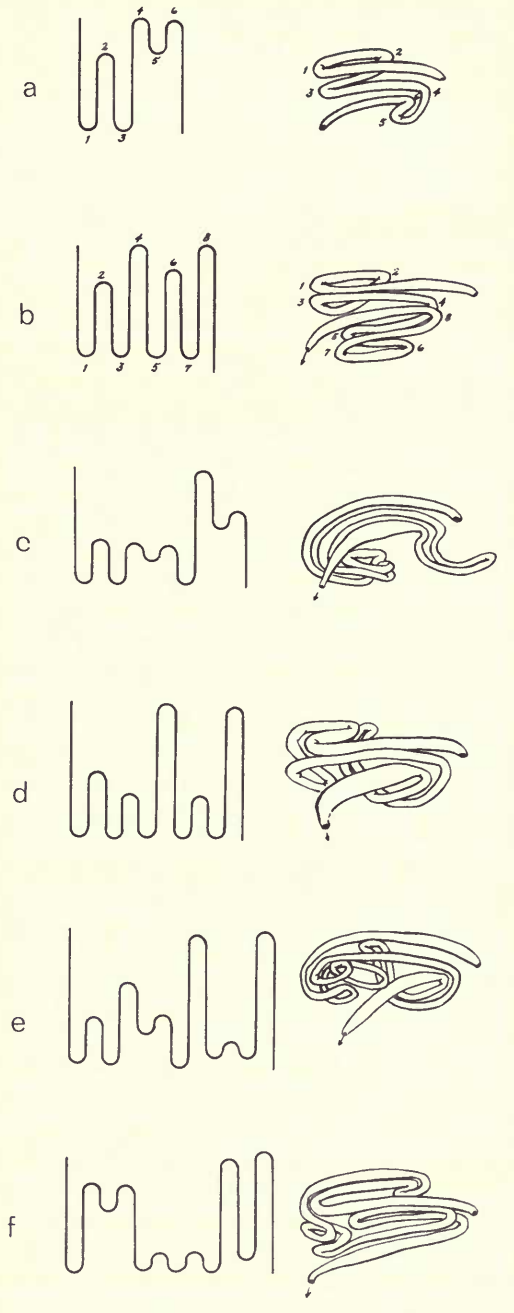


FIGURE 8. Diagrammatic exploded view of intestines of *Coryphaenoides anguliceps* showing bending patterns at left (note that bending numbers do not correspond with those of Okamura 1970*b*): (a) CAS 55832 (54.0 mm HL); (b) CAS 55832 (61.5 mm HL); (c) LACM 33588 (67.0 mm HL); (d) SIO 59-265 (43.8 mm HL); (e) SIO 59-265 (59.7 mm HL); (f) CAS 55182 (111 mm HL).

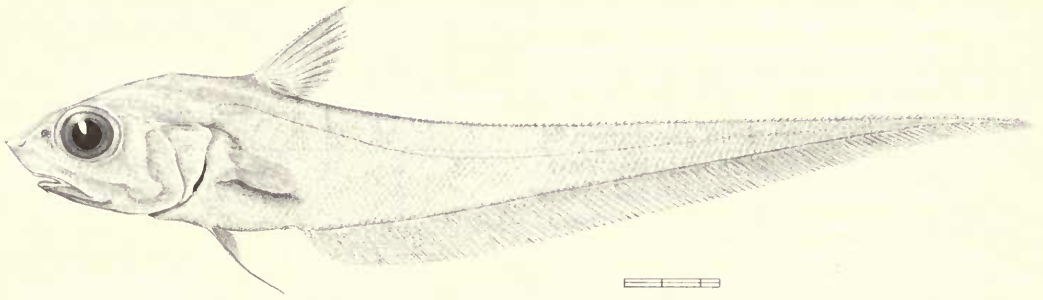


FIGURE 9. *Coryphaenoides ariommus.* CAS 55834, 55.3 mm HL, 270 mm TL, from off Chile in 1,170–1,480 m. Scale bar equals 25 mm.

numerous anatomical and mensural features. The shape of the head bones, the gills and associated structures, the mouth, barbel, dentition, and fins show obvious similarities. The two species can be readily distinguished by differences in squamation on the interorbital region (fewer, larger scales in *C. anguliceps*; see Fig. 5); extent of naked areas on the snout and suborbital region (more extensive in *C. anguliceps*); scales along the orbital rim and suborbital ridge (weak and deciduous in *C. anguliceps,* relatively strong and adherent in *C. ariommus*); modal differences in pelvic fin ray counts (mode = 8 in *C. anguliceps,* 9 in *C. ariommus*); spinulation of scales; and several morphometric measurements (see Table 1 and Fig. 7).

Coryphaenoides anguliceps is easily distinguished from *C. carminifer* by (among other features) the particularly stout mental barbel in the latter species and its coarser, more adherent scales. The group of species including *C. capito, C. myersi,* and *C. boops* differ considerably from *C. anguliceps* in its members having a shorter blunter snout, smaller gape, larger orbits, and a generally much different physiognomy.

Coryphaenoides ariommus Gilbert and Thompson, 1916

(Figures 4a, 5b, c, 9–11)

Coryphaenoides ariommus Gilbert and Thompson, 1916:471–472, pl. 5, fig. 1 (off Lota, Chile). Pequeño 1971:287–288, fig. 12 (descr. after Gilbert and Thompson 1916).

MATERIAL EXAMINED.—Holotype: USNM 76859 (58.5 mm HL, 250+ mm TL); 38°08′S, 75°53′W; 677 fm (1,238 m); ALBATROSS sta. 2791; 14 Feb. 1888. Paratypes: USNM 76891 (4: 58.5–79.3 HL, 235–340+ TL) and CAS-SU 22728 (7: 54.2–79.0 HL, 160+–300+ TL); same collection data as for holotype.

Other material.—PERU.—CAS 55835 (15 of 44: 35.0–77.9 HL, 135+–311+ TL) and MMSU P-16516 (6 spec.); 4°10′S, 81°27′W; 1,815–1,860 m, ANTON BRUUN, cr. 18B, sta. 766 (field no. LWK66-115); 9 Sep. 1966.—MMSU P-16521 (1: 32.3 HL, 133 TL); 7°50.5′S, 80°58.2′W; 2,400–2,600 m; AKADEMIK KURCHATOV sta. 1471, 3 Mar. 1971.—MMSU P-16522 (1: 71 HL, 297 TL); 9°56′S, 79°26.6′W; 891 m; DMITRY MENDELEEV sta. 544; 30 July 1972.—CAS 51798 (2: 56.0–62.1 HL, 233+–275+ TL) and MMSU P-16529 (4: 53.9–86.0 HL, 214+–356+ TL); 14°44′S, 76°12′W; 1,495 m; DMITRY MENDELEEV sta. 1654; 19–20 Mar. 1978.—IMARPE uncat. (1: 58 HL, 239 TL); 17°05.0′S, 72°16.9′W, 1,000 m; coll. L. Flores & L. Curotto, cr. 7201, sta. 7; 27 Jan. 1972.—SIO 72-184 (1: 53.7 HL, 216+ TL); 18°40′30″S, 70°36.0′W, 420–529 fm (768–967 m); THOMAS WASHINGTON field no. MV72-II-27.—SIO 72-183 (3 of 8: 27.3–64.1 HL, 100+–275 TL); 18°42.6′S, 70°37.9′W, 600–630 fm (1,907–1,152 m); field no. MV72-II-26; 7 May 1972. CHILE.—CAS 55833 (14: 54.1–84.0 HL, 250+–380+ TL), MMSU P-16515 (2 spec.), and USNM uncat. (2: 51–83 HL; 222+–370+ TL); 24°29.5′S, 70°40′W; 950 m; 72-ft otter trawl; ANTON BRUUN cr. 18A, sta. 714 (field no. LWK66-60); 16 Aug. 1966.—CAS 55834 (16: 40.8–75.0 HL, 188+–320+ TL); 33°39′S, 72°09.5′W; 1,170–1,480 m; 72-ft otter trawl; ANTON BRUUN cr. 18A, sta. 699 (field no. LWK6-41); 10 Aug. 1966.

DIAGNOSIS.—A species of *Coryphaenoides,* subgenus *Coryphaenoides,* with 1D. II,8–9 (rarely 7 or 10); 1P. i19–i26 (usually i20–i22); V. usually 9 (rarely 8 or 10); scales generally absent on lower portion of snout, most of interopercle, and leading margin of snout; 12–15 rows of scales across interorbital space; spinules on body scales short, conical in young, more triangular and flattened in adults, arranged in generally parallel, longitudinal rows; spinules obsolescent along posterior margin of exposed field in larger individuals; pyloric caeca slender, well developed, 9–13, directed anteroventrally for the most part; preopercular ridge forms an inverted clublike projection.

COUNTS AND MEASUREMENTS (75 spec.) (see

Table 1 for other counts).—A. and 2D. about 100–105; GR-1 (2–5) / (1–2) + (0–1) + (7–8) [8–10 total], GR-2 1 + (0–1) + (6–8) [7–10 total] / (1–2) + (0–1) + (5–8) [7–9 total]; scales 1D. 7–9 (18 spec.), 2D. 5–7.5 (8 spec.), mid-1D. 4.5–6.5 (15 spec.), lat.l. 41–55 (23 spec.); precaud. vert. 12 (one spec.); caeca 9–13 (22 spec.).

Total length 100+–380+ mm; HL 27.3–84.0 mm. The following in percent of head length: postrostral 69.0–75.7; snout 28.0–35.2; preoral 15.0–23.7; internasal 19.4–26.7; interorbital 20.1–29.4; orbit 25.1–36.1; suborbital 11.1–15.1; postorbital 36.8–46.8; orbit–preop. 35.9–43.4; upper jaw 24.8–30.9; rictus 16.8–21.4; barbel 4.1–8.6; gill slit 3.9–8.1; pre-D. 109–123; pre-A. 137–167; pre-V. 103–124; V.–A. 32–54; isth.–A. 61–93; 1D.–2D. about 20–50; 1D. 48–64; 1P. 40–51; V. 31–54.

Description.—Head robust, about as broad across preopercle as depth at hind edge of orbits, length 4.3–5.1 into TL. Orbits large, diameter 3–4 into HL, usually about equal to snout length, but orbit : snout ratio variable (0.75–1.24); dorsal rim forms part of head profile. Snout broad, tipped with a small spiny tubercle and flanked by similar but blunter tubercles at lateral angles, width across supranarial ridges slightly less than that of broad, slightly concave interorbital space. Mouth moderate in size and inferior, lateral opening restricted by lip folds, rictus extends to below anterior edge of orbits, maxillary extends to about middle of orbit; distance end of rictus to posterior end of maxillary usually more than barbel length. Barbel small, slender, length less than twice posterior nostril length. Suborbital region divided into upper and lower halves by a well-developed longitudinal shelf, but shelf ridge not sharply edged with spiny, scutelike scales. A series of prominent neuromasts parallel lower anteroventral edge of orbits, with a series branching off below nostrils. Preopercle margin broadly rounded; vertical and horizontal ridges of bone meet posteroventrally in a club-shaped projection. Posterior edge of interopercle narrowly exposed beyond preopercle margin and smoothly joined with subopercle and opercle to form posterior edge of gill cover.

Gill membranes thick, closely attached along entire length of isthmus, without a free posterior fold; point of attachment with isthmus under vertical ridge of preopercle. Slits between gill arches restricted dorsally and ventrally; outer gill slit greatly restricted, length about the same as barbel length (but much variation in both measurements). Outer gill rakers of first arch few (2–5), rudimentary, and scarcely visible; others tubercular with several projecting, recurved, needlelike spinules. Gill filaments short, longest on first arch about equal to length of outer gill slit.

In a 55-mm-HL specimen from Chile (CAS 55834) close in size to the holotype, dorsal snout and interorbital surfaces almost completely covered with small scales, each with 1–6 slightly divergent rows of small, erect, slender, needlelike spinules. Anteriormost leading dorsal edge and almost all of ventral snout surface naked (except for a few small, thin, isolated scales). Tubercular scutes at tip and lateral angles of snout prominent but rather blunt. A distinct series of small, adherent, scutelike scales along dorsal edge of orbit, connecting to similar series over supranarial ridge. A series of similar but smaller and widely spaced scales deeply embedded in thick, fleshy skin along suborbital shelf, aligned above and not forming part of ridge. Suborbital shelf otherwise naked below anterior ⅔ of orbit; more posteriorly, shelf covered with small scales blending in with those on preopercle. On ventral portion of suborbital, squamation extends in a broad wedge from preopercle anteriorly to level of posterior nostril. Ventral margin of suborbital naked. Area surrounding nostrils, including adjacent rim of orbit, naked. Mandibular rami covered along posterior ⅔ by small thin scales, but naked anteriorly. Nape scales with spinule rows slightly more divergent than those on head scales, and spinules somewhat more flattened and reclined. Scales on trunk thin, deciduous, with brittle, needlelike spinules arranged in 5–10 subparallel rows. Those immediately below dorsals with spinules mainly on anterior part of exposed field and only low ridges on broad posterior margin.

In a somewhat larger specimen (CAS 55834, 71 mm HL), squamation on head much the same as on smaller individuals but more scales below nostril region, and ventral snout surface and anterodorsal edge of snout covered with short, blackish, hairlike papillae. Larger scales below dorsals have 12–13 rows of short spinules that are either more angular in cross section than those of smaller individuals or are more flattened and leaflike (Fig. 4a).

In an even larger specimen (CAS 55833; 79

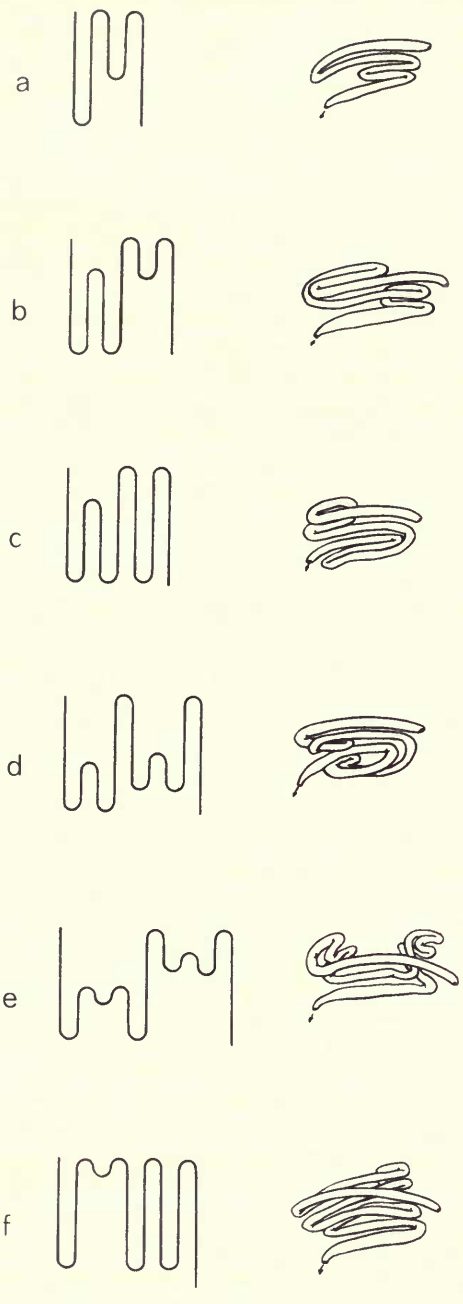


FIGURE 10. Diagrammatic exploded view of intestines of *Coryphaenoides ariommus* showing bending patterns at left: (a) CAS 55833 (58.0 mm HL); (b) CAS 55833 (59.0 mm HL); (c) CAS 55835 (76.4 mm HL); (d) CAS 55835 (47.0 mm HL); (e) CAS 55835 (77.9 mm HL); (f) CAS uncat. (98 mm HL).

mm HL), head even more scaled, including leading snout edge and almost all of ventral suborbital region to below anterior nostril.

Dentition in both jaws composed of small conical, recurved teeth set in cardiform bands, none of teeth notably enlarged, although outer ones tend to be larger than inner ones. Premaxillary band about 5–6 rows wide, abruptly narrowing at posterior end, which coincides with end of rictus. Dentary band narrow, 2–3 teeth wide; individual teeth generally smaller than corresponding premaxillary teeth; band extends slightly farther back into mouth than premaxillary band.

First dorsal fin ray a small spike protruding at base of second ray, which is relatively short (greatest length much less than postrostral length of head), triangular in cross section, and armed along its leading edge with small serrations that become obsolescent basally in large specimens. Second dorsal fin rudimentary throughout; anteriormost rays in larger individuals often obsolescent. Pectorals broad but short, barely reaching vertical through anal fin origin. Pelvics short, small, outermost ray extended into hair-fine tip that barely reaches past anal fin origin; all other rays of fin fall well short of anus. Pectoral and pelvic origins about on same vertical, that of first dorsal slightly posterior.

Intestinal coiling variable among specimens examined; pattern ranged from simple (see in CAS 55833, 58 mm HL; Fig. 10a) to the more commonly encountered pattern in another specimen (59.0 mm HL; Fig. 10b) from the same collection, to more convoluted (Fig. 10c–f). These intraspecific differences transcend Okamura's (1970*b*, fig. 68) different stages of intestinal coiling within the *Coryphaenoides* and *Coelorinchus* lines, and take the extreme of *Coelorinchus* (Okamura's fig. 68J) a step or more further.

Pyloric caeca slender, unbranched, usually directed anteriorly at base but distally sweeping down and around anterior end of pyloric portion of stomach; length about half orbit diameter. Swim bladder large; drumming muscles well developed in males examined, but not in females. Retia 4, long, slender, convoluted, terminating in 4 gas glands that are paired into 2 flattened, bean-shaped masses, each gas gland closely adhered to its fellow.

Color in alcohol light brown to tawny over scaled regions in Nazca Ridge specimens, but darker in other specimens. In areas with missing scales, integument whitish to flesh colored and

scale pockets outlined in brown. Normally scaleless parts of head dirty brownish. Lips and barbel dark brown. Branchial and peritoneal membranes blackish, oral membrane dark gray to blackish. Gill arches and rakers dusky to blackish, gill filaments pale. Fins dusky to blackish.

DISTRIBUTION (Fig. 11).—Northern Peru (4°10′S) to southern Chile (38°08′S) in 768–1,860 m.

REMARKS AND COMPARISONS.—Of the eastern Pacific species, *Coryphaenoides ariommus* is most likely to be confused with *C. anguliceps,* a species with which it is sympatric off northern Peru (ANTON BRUUN cr. 18B, sta. 115), although the primary distribution of *C. ariommus* is south of that area and that of *C. anguliceps* is to the north. The two species share in common a generally similar physiognomy, a closeness in morphometric proportions and meristic counts, and similarities in such features as dentition, restriction of gill membranes, gill raker shape, alimentary canal coiling, and various squamation features. They are readily distinguished by a combination of characters including: pelvic fin ray count (usually 9 in *C. ariommus,* 8 in *C. anguliceps*); color of mouth (blackish or dark gray in *C. ariommus,* pale or light gray in *C. anguliceps*); scale rows across interorbital space (11–14 in *C. ariommus,* versus 6–8); coarse, adherent row of scales over supranarial and supraorbital ridges in *C. ariommus* (lacking in *C. anguliceps,* or at least none in specimens examined); length of rictus (16.9–20.9 percent HL in *C. ariommus* versus 22.7–26.2); a somewhat broader interorbital space and larger orbits in *C. ariommus* (see scatter diagrams, Fig. 6). In addition to these characters, *C. ariommus* has smaller body scales than does *C. anguliceps,* but because of the denuded and often damaged condition of most specimens, the differences could not be enumerated. *Coryphaenoides ariommus* also has a wider head than does *C. anguliceps*; spinules on body scales in adults are flattened or more angular in cross section than the smoothly conical spinules of *C. anguliceps*; and none of the premaxillary teeth are enlarged, in contrast to the slightly enlarged outer teeth series in *C. anguliceps.*

Coryphaenoides ariommus is probably more distantly related to *C. boops* and *C. capito* than to *C. anguliceps.* Differences in counts, squamation on the head, shape and relative sizes of opercular bones and pyloric caeca, and shape of snout and suborbital regions are notable.

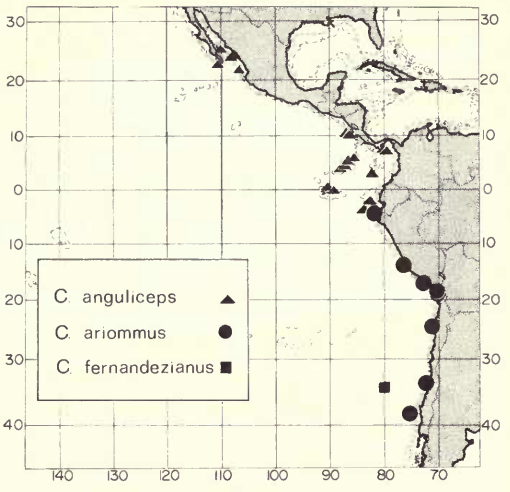


FIGURE 11. Map showing distributions of *Coryphaenoides anguliceps, C. ariommus,* and *C. fernandezianus.*

Coryphaenoides boops (Garman, 1899)

(Figures 4b, 12–15)

Macrurus boops Garman, 1899:202–203 (type locality off Panama, ALBATROSS sta. 3356 in 511 fm [935 m] and sta. 3394 in 546 fm [999 m]).

Coryphaenoides boops: Gilbert and Hubbs 1916:143 (list).

MATERIAL EXAMINED.—Lectotype (here designated): MCZ 28588 (male, 47.2 mm HL, 203 mm TL); Gulf of Panama, 7°21′N, 79°35′W; 511 fm (935 m); ALBATROSS sta. 3394; 10 Mar. 1891. Paralectotypes: MCZ 61093 (2: 41.9–46.7 HL, 172–192 TL) (smaller spec. is a *C. capito*); same local. data as for lectotype.—Paralectotype: MCZ 28587 (1: 57.9 HL, 245+ TL) (this is a spec. of *C. capito*); SW of Punta Mala, Panama; 7°09′30″N, 81°08′30″W; 322 fm (999 m); ALBATROSS sta. 3356; 23 Feb. 1891.

Other material.—ECUADOR.—USNM 148996 (4: 52.8–73.7 HL, 248–300+ TL); 00°37′N, 81°00′W; 401 fm (750 m); ALBATROSS sta. 2792; 2 Mar. 1888.—CAS 38350 (3: 84.2–97.2 HL, 400–425+ TL); 3°15′S, 80°55′W; 945–960 m; ANTON BRUUN cr. 18B, sta. 770; 10 Sep. 1966. PERU.—IMARPE uncat. (1: 83.5 HL, 360+ TL); 3°39′S, 81°22′W: 720 m.—IMARPE uncat. (1: 55.9 HL, 272 TL); 3°48.2′S, 81°22′W; 700–750 m.—LACM uncat. (1: 81.5 HL, 350+ TL); 6°42′S, 80°59′05″W; 780 m; beam trawl; sta. SNP1-25; 22 Jan. 1974.—MMSU P-16530 (1: 62.2 HL, 253+ TL) and CAS 50955 (1: 64.1 HL, 302 TL); 7°41′S, 80°40′W; 900–1,000 m. IKMT on bottom at 900 m; AKADEMIK KURCHATOV sta. 1472; 4 Mar. 1972.—CAS 55836 (3: 29.6–57.2 HL, 158–250+ TL); 7°49′S, 80°38′W; 605–735 m; ANTON BRUUN cr. 18B, sta. 754 (field no. LWK66-93); 5 Sep. 1966.

DIAGNOSIS.—A species of *Coryphaenoides,* subgenus *Coryphaenoides,* with 1D. II,8–9, 1P. 21–25; V. 7–8; chin barbel short but relatively thick; scales generally absent on lower portion of snout, ventral margin of preopercle, most of interopercle, and anteriorly on lower jaw; leading

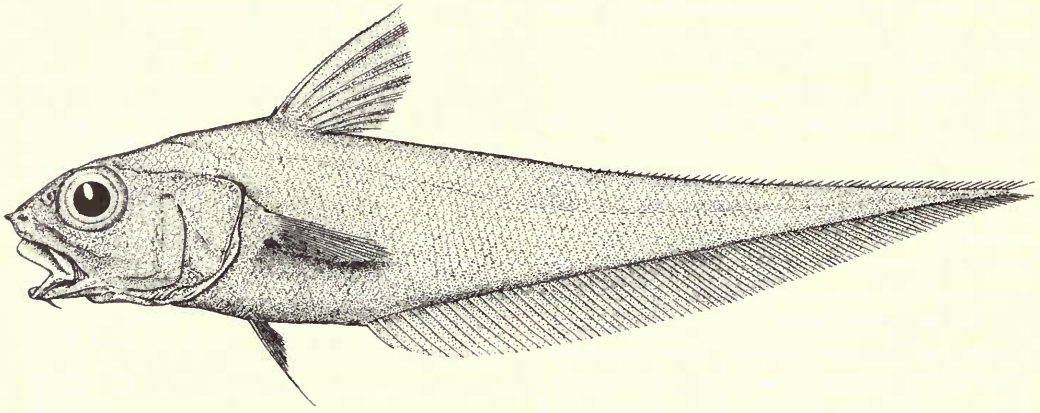


FIGURE 12. *Coryphaenoides boops.* MMSU P-16530 (62.2 mm HL, 253+ mm TL) from off Peru, 900 m.

dorsal margin of snout narrowly naked; scales on suborbital shelf in 2–3 rows, scales not modified into heavy scutes nor elongated in a longitudinal line; all scales rather strongly adherent; spinules on scales dense, long, slender, reclined, arranged in irregular quincunx or widely divergent or convergent pattern; pyloric caeca stublike, 6–7, directed anteriorly.

COUNTS AND MEASUREMENTS (13 specimens).—D. II,8–9 + about 116; 1P. i20–i24; V. 7 (sometimes 8); GR-1 (3–6)/(1–2) + (0–1) + (9–10) [10–12 total], GR-2 1 + (0–1) + (8–10) [9–11 total] / (1–2) + (0–1) + (7–8) [9–11 total]; scales 1D. 6.5–8, 2D. 4.5–6.5, mid-1D. 3.5–6.5, lat.l. 31–38; caeca 6–7.

Total length 158–360+ mm; HL 29.6–83.5 mm. The following in percent HL: postrostral 75.4–77.6; snout 25.1–27.2; preoral 8.3–12.8; internasal 12.6–14.9; interorbital 14.0–16.9; orbit 29.4–34.5; suborbital 7.8–9.8; postorbital 40.8–49.2; orbit-preop. 31.5–35.6; upper jaw 29.7–34.0; nostril 4.7–7.5; barbel 5.9–10.0; gill slit 7.2–

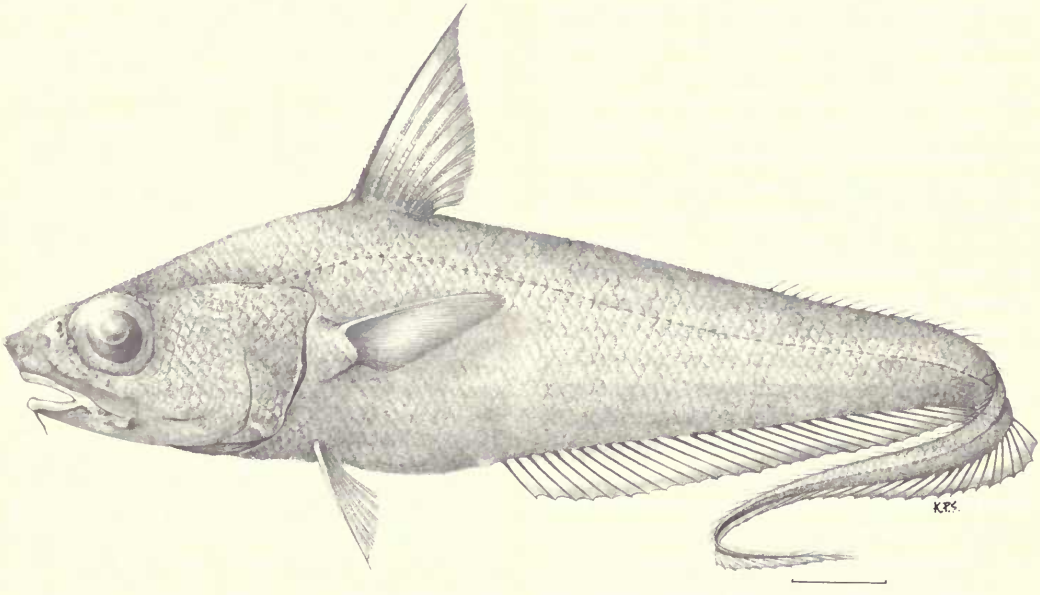


FIGURE 13. *Coryphaenoides boops.* CAS 38350 (84.2 mm HL, 400 mm TL) from off Gulf of Guayaquil, Ecuador, in 945–960 m. Scale bar equals 25 mm. Drawn by Katherine P. Smith.

10.5; pre-D. 109–127; pre-A. 138–178; pre-V. 102–131; V.–A. 34–70; isth.–A. 69–109; body depth 66–89; 1D.–2D. 28–48; 1D. 58–76 (5 spec.); 1P. 52–62; V. 33–47.

DESCRIPTION.—Body stout, greatest depth at dorsal origin about equal to postrostral length of head, tapers rapidly behind vent to end of tail; head about 4.0–4.5 into TL. Head stout, rather conical in shape, about as high as wide at posterior orbit margin. Orbits large, basically round in outline, about 3.0–3.2 into HL, greater than snout length, deeply incised into top of skull, resulting in narrow interorbital space, which goes about 2.0–2.2 into orbit diameter. Snout low, barely protruding beyond mouth; tip armed with a single stout, spinous, conical scute; lateral snout angles with 1 or 2 stout but blunt scutes. Mouth opening restricted laterally; rictus barely extended posteriorly to anterior edge of orbits. Barbel short, stout at base, tapering rapidly to fine tip. Suborbital region narrow, demarcation into upper and lower parts distinct but not especially sharp. Preopercle broadly rounded; chord of posterior margin nearly vertical; vertical and horizontal ridges meet at a near right angle without a lobelike projection at angle. Opercle and subopercle broadly exposed, their posterior margins smoothly continuous with posterior margin of broadly exposed interopercle.

Gill membranes thick, broadly attached to isthmus; gill openings on each side restricted, completely separated from each other. Gill rakers small, tubercular; filaments long; longest on first arch almost half orbit diameter. Openings between gill arches much restricted. Spines on rakers of third and fourth arches notably long.

Body scales rather large, densely covered with greatly reclined, sharp, slender, conical spinules arranged variably in essentially parallel rows (12–14 rows in one syntype 45.7 mm HL) to irregularly quincunx to widely divergent "V" pattern, the spinules giving a coarse texture to surfaces. Head scales generally similar to those of body, but spinules shorter and more erect. Scales along head ridges somewhat stouter and more adherent, but not especially enlarged or scutelike except at tip and lateral angles of snout where stout, tuberclelike scutes obtain. Scales on suborbital shelf strongly adherent, small but stout, in 2–3 irregular rows below anterior half of orbits and forming a well-defined dorsal border. Spinous scales uniformly cover most of dorsal surfaces of head. Snout essentially naked ventrally and along leading upper margin (a few small isolated scales in some specimens), the naked area extending posteriorly along ventral portion of suborbital. Small scales intrude from posteriorly onto ventral surface of suborbital, and a patch of small scales below and behind lateral snout angle in some specimens. Mandibular rami almost entirely naked except near posterior end where scattered small scales prevail. A series of small pores along middle of each ramus, in addition to scattered papillae of free neuromasts. Ventral margin of preopercle and ventral arm of preopercular ridge naked. Naked surfaces of snout and suborbital covered with small papillaelike free neuromasts; these also scattered over scaled portions of suborbital, snout, and interorbital space. Broad circular area around nostrils naked, including rim of orbits adjacent to posterior nostril; adjoining suborbital shelf area broadly scaled.

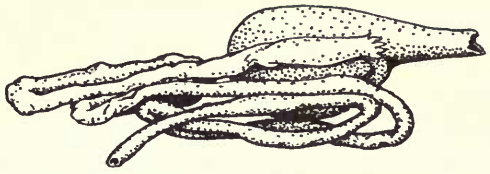


FIGURE 14. Slightly exploded right lateral view of alimentary canal of *Coryphaenoides boops* drawn from a paratype, MCZ 18588 (46.7 mm HL). Proportions and relationship of intestines to stomach altered for clarity.

Teeth in both jaws small, slender, conical, slightly recurved, arranged in bands that gradually taper posteriorly. Premaxillary band about 7–8 teeth wide anteriorly, dentary band about 4 teeth wide. Both upper and lower teeth bands extend posteriorly into mouth slightly beyond rictus. No teeth enlarged.

First dorsal fin relatively low and short; first spinous ray a short spike closely adhered to long second spinous ray, which is triangular in cross section near base with a weakly serrated leading edge. Interspace between dorsals wide, about equal to postrostral length of head; second dorsal poorly developed throughout. Pectoral and pelvic origins about on same vertical; that of first dorsal slightly behind. Pectorals broad but short, extending posteriorly to above first 1 or 2 anal rays. Pelvics small, outermost ray hairfine distally, barely reaching vent.

Alimentary canal (Fig. 14) multiply looped, similar to that illustrated by Okamura (1970b: 120, fig. 63D) for *C. marginatus* except that loop

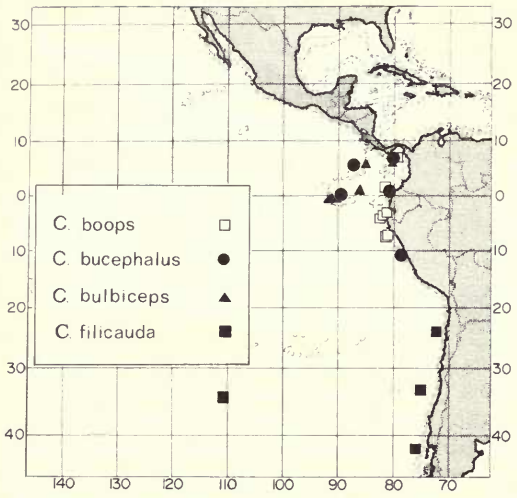


FIGURE 15. Map showing eastern Pacific distributions of *Coryphaenoides boops, C. bucephalus, C. bulbiceps,* and *C. filicauda.*

formed by Okamura's "bend 2" (folding around front and left side of stomach) much longer in *C. boops.* Pyloric caeca rudimentary, stublike, 6 or 7 directed anteriorly. Swim bladder well developed, with 4 small gas glands, each connected to a long slender rete. Anus immediately anterior to anal fin, without intervening scales.

Color in alcohol overall dark brownish to swarthy, fins blackish to swarthy. Gill cavity black; oral cavity dark gray. Branchiostegal membranes and naked areas on head grayish with violet tinge, paler on gular membrane. Barbel blackish on base, abruptly paler on distal half.

DISTRIBUTION (Fig. 15).—Panama to northern Peru, at depths of 605–1,000 m.

REMARKS AND COMPARISONS.—*Coryphaenoides boops* and its eastern Pacific congeners *C. capito* (Garman, 1899) and *C. myersi* n. sp. form a closely related group having in common: (1) relatively low, broad head; (2) protrusible jaws with long ascending premaxillary process, coupled with laterally restricted mouth opening, the rictus not extending much behind anterior edge of orbits; (3) a short barbel; (4) gill membranes closely attached to isthmus greatly restricting opercular openings; (5) surfaces of head with prominently developed cephalic sensory canal system; (6) broadly rounded preopercle, posterior margin nearly vertical, preopercle ridge not lobelike or much produced at angle; (7) snout bluntly pointed, extending little beyond mouth; (8) suborbital region smoothly rounded, lacking stout, enlarged, scutelike scales along ridge; (9) jaw teeth all small, in narrow bands; and (10) first gill slit greatly restricted, almost porelike, diameter much less than half orbit diameter.

Many of these features are shared with the species group including *C. semiscaber* Gilbert and Hubbs, 1920, *C. marginatus* Steindachner and Döderlein, 1887, *C. microps* (Smith and Radcliffe, 1912), *C. macrolophus* (Alcock, 1889), and *C. tydemani* (Weber, 1913) which Gilbert and Hubbs (1920:413) characterized as ". . . a well-marked group of species which agree in possessing a produced dorsal spine, a deep and sharply compressed body, and a dorsal contour horizontal behind the first dorsal fin."

Coryphaenoides boops appears most closely related to *C. capito,* with which it is apparently sympatric. The difficulty in distinguishing between these two very similar species led to Garman's mixing individuals of both species in the type series for *C. boops.* Thus, at ALBATROSS station 3394 in the Gulf of Panama, one of three syntypes of *C. boops* was actually a specimen of *C. capito,* as was the single syntype (MCZ 28587) from station 3356. We here designate the 47.2 mm HL male from sta. 3394 as the lectotype of *C. boops.*

The main features distinguishing *C. boops* from *C. capito* are: (1) scales more adherent in *C. boops*; (2) suborbital shelf scales round or oval, in three or four rows, versus. somewhat elongated, in one deeply embedded row in *C. capito*; (3) spinules long, needlelike, curved, moderately reclined, and densely packed, versus in *C. capito,* spinules short, very slender and weak, erect, and widely spaced (in larger specimens, spinules either mostly broken off or obsolescent, and in some, scales without spinulation, with only low ridges on exposed fields); (4) scales on first dorsal base scarcely extend up onto fin (although sometimes a single row of tiny scales basally on shank of second spinous ray, as in *C. capito*), versus small deciduous scales that extend notably up fin in *C. capito*; (5) pelvic rays usually seven, sometimes eight, versus eight or nine in *C. capito*; and (6) orbits at all sizes essentially circular, with anteroventral corner well defined, versus orbit shape more ellipsoid in larger specimens of *C. capito* with longest axis anteroventral-to-posterodorsal, the anteroventral corner extended, fleshy, the margin ill-defined.

The larger specimens we examined clearly show

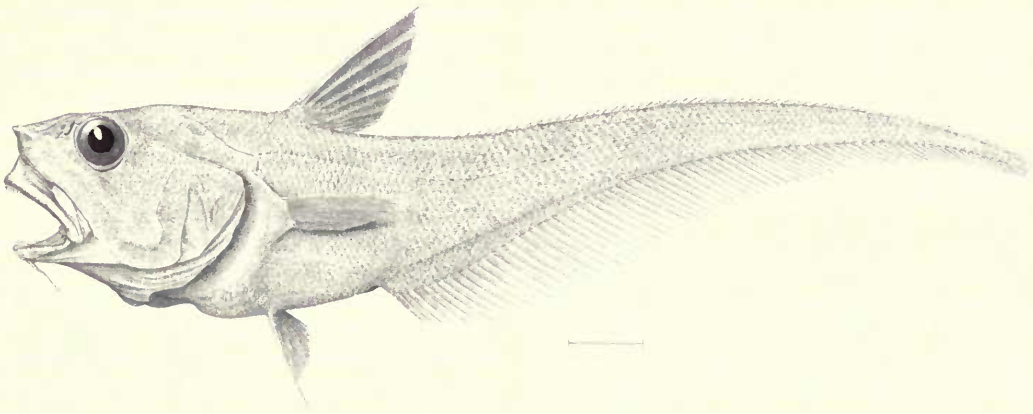


FIGURE 16. *Coryphaenoides bucephalus.* MMSU P-16531 (83.7 mm HL, 345+ mm TL) from off Peru in 2,290–2,230 m. Scale bar equals 22 mm.

the strongly different physiognomy of the two species. Particularly notable are the distinctly humpbacked appearance of *C. capito,* its elongate orbits, smaller terminal and lateral snout scutes, single row of suborbital scales, and the generally denuded state of preserved specimens. Smaller *C. capito* (e.g., MCZ 61093, 41.9 mm HL; CAS 43981, 33.5 and 35.6 mm HL, from Costa Rica; and CAS 55839, 45.8 mm HL, from Ecuador) are not so distinct, especially if the *C. capito* specimens are denuded of scales. General proportions do not differ significantly (in fact proportional measurements and all but the pelvic fin ray counts are essentially identical in the two species); the orbits are circular in small *C. capito* as in *C. boops*; the scales on the suborbital appear to be almost the same size; the terminal and lateral snout scutes are of similar size; the humpback is not developed; and the scales on the suborbital of small *C. capito* are more numerous and denser than those of larger individuals, approaching the condition found in *C. boops.*

Coryphaenoides boops is closely similar to *C. carminifer,* and the distributions of the two species broadly overlap, although they have not been captured together. Similarities lie in the general structure of the head, snout, jaws, gill cover, gills, and fins. Like *C. boops, C. carminifer* has a blunt snout that protrudes little beyond the mouth and is armed with a heavy terminal scute; the rictus is restricted posteriorly and extends to below the anterior orbital margin; the preopercle is broadly rounded as in *C. boops,* but its ridge has a lobular prolongation at the angle; the interopercle is exposed and scaled posteriorly; and papillae of the cephalic sensory canal system are numerous and well developed, especially on the snout. Numerous other similarities exist that show a fundamental relationship between the two species. *Coryphaenoides carminifer* differs from *C. boops* in having an overall much thicker barbel; no naked areas on snout; a thick, greatly prolonged outer pelvic ray; spinules on scales in parallel rows; and long slender pyloric caeca.

Coryphaenoides boops shows relationships with *C. myersi* in general features, but the two are readily distinguished by differences in pelvic ray counts and the extent of development of the outer pelvic ray. Other differentiating features are given in the description of *C. myersi.* Relationships of *C. boops* to other eastern Pacific members of the genus are remote, and its ties (as with *C. myersi* and *C. capito*) are probably closer to Indo-Pacific species of the *C. semiscaber* species group.

Coryphaenoides bucephalus (Garman, 1899)

(Figures 4c, 15, 16)

Macrurus bucephalus Garman, 1899:195–196 (type locality off Panama, Cocos, and Ecuador).

Coryphaenoides bucephalus: Gilbert and Hubbs 1916:143 (list).

TYPE SPECIMENS.—Lectotype (here designated): MCZ 28599, 94.8 mm HL, 350+ mm TL; Gulf of Panama, 7°15′N, 79°36′W; 1,020 fm (1,865 m); ALBATROSS sta. 3393; 10 Mar. 1891. Paralectotypes: MCZ 28590 (1: 124 HL, 590+ TL); Cocos Ridge, 5°36′40″N, 86°56′50″W; 134 fm (245 m); ALBATROSS sta. 3370; 28 Feb. 1891; by tangles [see Remarks].—MCZ 28601 (2: 65.0–75 HL, ?–330+ TL); Ecuador, 1°07′N, 80°21′W; 1,573 fm (2,877 m); ALBATROSS sta. 3398; 23 Mar. 1891.—MCZ

28600 (1: 46.4 HL, about 220 TL); off Mazatlan, Mexico; 23°16'N, 107°31'W; 852 fm (1,558 m); ALBATROSS sta. 3430; 19 Apr. 1891 (paratype of *Coryphaenoides oreinos* Iwamoto and Sazonov, n. sp.).

Other material.—GALAPAGOS.—USNM 150192 (2: 106–124 HL, 430+–570+ TL); 0°24'S, 89°06'W; 812 fm (1,485 m); ALBATROSS sta. 2807; 4 Apr. 1888. PERU.—MMSU P-16531 (1: 83.7 HL, 345+ TL); 10°53'S, 78°46'W; 2,290–2,230 m; DMITRY MENDELEEV cr. 20, sta. 1648; 15 Mar. 1978.

DIAGNOSIS.—A species of *Coryphaenoides*, subgenus *Coryphaenoides*, with 1D. II,8–9; 1P. i19–i23; V. 9; teeth prominent, those on premaxillary in a band with outermost series notably large, mandibular teeth in a single row except at symphysis; ventromedian area below snout tip naked, head otherwise without naked areas; terminal and lateral snout scutes weak or not developed; suborbital region and other head ridges without modified scutelike scales.

COUNTS AND MEASUREMENTS (7 specimens).—1D. II,8–9; 1P. i19–i23; V. 9 (1 spec. had 8 on left fin and 9 on right, but left fin appeared somewhat abnormal); GR-1 (1–2) + (0–1) + (7–9) [9–10 total], GR-2 (1–2) + (0–1) + (7–8) [9–10 total]; scales 1D. 7.5–9, 2D. 5.5–7, mid-1D. 4.5–5.5, lat.l. 34–38 (4 spec.).

Total length 330+–590+ mm; HL 65.0–124 mm. The following in percent HL: postrostral 72–75; snout 26–30; preoral 11–16; internasal 20–21; interorbital 23–28; orbit 23–26; suborbital 12–15; postorbital 47–53; orbit–preop. 44–49; upper jaw 38–44; nostril 5.1–5.9; barbel 17–23; gill slit 8–9; pre-D. 106–111; pre-A. 152–164; pre-V. 102–115; V.–A. 48–62; isth.–A. 87–106; body depth 75–78; 1D.–2D. 15–30; 1D. 53–60; 1P. about 50; V. 40–53.

DESCRIPTION.—Head broad, greatest width more than depth behind orbit; HL about 3.7–4.8 into TL. Orbits round, relatively small, horizontal diameter less than snout length and interorbital space, about 4.5 in HL. Interorbital region flat to slightly depressed in preserved specimens, but probably slightly convex in life. Snout low, bluntly pointed with a single weakly spined terminal scute; lateral angles rounded and lacking scutes. Mouth large, unrestricted laterally; with jaws closed, rictus extends posteriorly almost to or below middle of orbits; hind end of maxilla extends to below posterior ⅓ of orbit. Barbel slender, of moderate length (about 1.0–1.4 into least suborbital width). Suborbital region vertical, gently rounded, without a pronounced longitudinal ridge separating upper and lower portions in well-preserved specimens; squamation differences delineate the 2 regions, however. Preopercle large, somewhat produced posteroventrally into a slight lobe; preopercle ridge forms a prominent lobe. Opercle and subopercle of moderate size; their posterior margins smoothly blended and forming an almost straight or steeply declined edge before rounding off at interopercle, of which only the posterior tip is exposed.

Gill membranes rather narrowly attached to isthmus (compared with *C. ariommus*, for example), without a free posterior fold. Outer gill arch greatly restricted by folds of skin connecting upper and lower arms to gill cover; the outer slit less than width of suborbital, about equal to length of longest gill filaments. Gill rakers blunt, tubercular, weakly spined.

Head and body almost completely and uniformly scaled except on fins and gill membranes. A small ventromedian area on snout, region immediately surrounding nostrils, and interopercle bone naked. Scales of head generally smaller than those of body and densely covered with minute, relatively erect slender spinules arranged in divergent rows. Scales on suborbital shelf slightly larger than those ventrally and with fewer, coarser spinules. Scales along median nasal, supranarial, and supraorbital ridges similarly different from surrounding scales, but generally poorly defined and not scutelike. Body scales (Fig. 4c) large, covered with relatively long, slender, erect, slightly recurved, conical spinules arranged in ill-defined longitudinal rows. Body surfaces coarsely textured.

Premaxillary teeth in a long, broad, gradually tapered band, widest part of band about 6–7 teeth deep. Inner teeth small, bordered externally by large, wide-spaced conical canines, the anteriormost being notably long (length of longest about equal to length of posterior nostril) and slightly recurved. Dentary teeth moderate sized, widely spaced, erect canines only slightly recurved and arranged in a single row except near symphysis where teeth scattered in 2 or 3 series. In smaller individuals (e.g., 65-mm and 75-mm HL specimens from MCZ 28601) dentary teeth smaller, in 2–3 irregular rows laterally and in a band 3–4 teeth wide near symphysis. Teeth in both jaws extend posteriorly well beyond rictus.

Generally poor condition of specimens examined precluded accurate assessment of fin sizes, but fins generally small to moderate in size. Spi-

nous second ray of first dorsal slightly prolonged into a fine tip, length slightly more than postorbital length; denticulations on leading edge weak, obsolescent basally. Second dorsal rudimentary throughout; anal well developed. Outer pelvic ray elongate, the long, hairfine tip extends slightly beyond anal fin origin; other rays of fin reach about halfway between origins of pelvic and anal fins, if that far. Origin of first dorsal slightly behind that of pectoral, which in turn is slightly behind that of pelvics; origin of second dorsal slightly before or behind that of anal.

Anus immediately before anal fin. Pyloric caeca in MCZ 28601 (75 mm HL) long (length about equal to least width between supranarial ridges), slender, about 14 total. Other alimentary canal features not determined because of poor condition of specimens.

Coloration in alcohol of MMSU specimen overall grayish brown, darker on abdomen, operculum and gill membranes. Fins and barbel dusky to gray-brown. Lips edged in black. Branchiostegal membrane, lining of branchial cavity, and peritoneum black. Oral cavity dark gray.

DISTRIBUTION (Fig. 15).—Gulf of Panama to Galapagos and northern Peru; 1,485–2,877 m.

REMARKS AND COMPARISONS.—Collection data for paralectotype MCZ 28590, reportedly taken by tangles in 134 fm (245 m), are suspect in that the depth is far too shallow and the gear somewhat questionable. The small paralectotype (MCZ 28600, 46.4 mm HL) from the Gulf of California off Mazatlan, Mexico, represents *C. oreinos* new species, described below.

Coryphaenoides bucephalus is readily distinguished from other congeners in the eastern Pacific by characters given in the Key and Diagnosis. The species differs from the presumably sympatric *C. bulbiceps* in (among other characters) having a naked ventral snout strip (none in *C. bulbiceps*); orbit diameter shorter than snout and interorbital (versus about equal to); large prominent canines on premaxilla (teeth all small in *C. bulbiceps*); coarsely spinulated scales (versus spinules very short, greatly reclined, giving a rather smooth surface texture in *C. bulbiceps*); and V. 9 (versus 8).

Relationships among the genus are inadequately known and little can be said about those of *C. bucephalus.* The species shows similarities in physiognomy to *C. filifer* (Gilbert, 1890) from the eastern North Pacific, but squamation features are quite different between the two. There are similarities in dentition and general shape to species of the subgenus *Chalinura,* but again, squamation features, especially that on the snout, differ. *Coryphaenoides longicirrhus* (Gilbert, 1905) from Hawaii is superficially similar but lacks the naked ventromedian area on the snout and has a broader band of mandibular teeth.

Coryphaenoides bulbiceps (Garman, 1899)

(Figures 3a, 15, 17)

Macrourus bulbiceps Garman, 1899:194–195, pl. XLIV, fig. 1, 1a (type locality off Cocos Ridge).

Nematonurus bulbiceps: Gilbert and Hubbs 1916:143 (list).

Coryphaenoides bulbiceps: MacDonald and Mudie 1974 (collected at surface after seismic disturbances fide Cohen and Haedrich 1983; ref. not seen).—Cohen and Haedrich 1983: 375 (photographic observations on Galapagos thermal vent region).

MATERIAL EXAMINED.—Holotype: MCZ 28602 (112 mm HL, 550+ mm TL); Cocos Ridge, 5°43′N, 85°50′W; 978 fm (1,789 m); ALBATROSS sta. 3363; 26 Feb. 1891.

Other material.—GULF OF PANAMA.—UMML uncat. (2: 63.0–68.8 HL, 295+–311+ TL); 6°53′N, 79°27′W; 3,193 m; PILLSBURY sta. 526; 5 May 1967. GALAPAGOS.—SIO 74-44 (133 HL, 660+ TL), off James I., 0°10.5′S, 90°55′W; 2,000 m; free-vehicle setline; ALPHA HELIX: fall, 1970.—SIO 72-108 (137 HL, most of tail missing); 0°48′N, 86°09.0′W; dipnetted on surface ("20–40 fishes floating near area of high seismic activity"); ALPHA HELIX; 26 June 1972.—CAS 42518 (15: 107.5–183.5 HL, 559+–810+ TL); 0°41′S, 91°35.5′W; 2,490 m; free-vehicle bottom setline; ANTON BRUUN cr. 16, sta. 618B; 26 May 1966.—CAS 55837 (12: 127–154 HL, 580+–732 TL); MMSU P-16517 (1: 131 HL, 650 TL), and USNM uncat. (2: 131–144 HL, 625+–645+ TL); 0°11.3′S, 91°27.2′W; 1,710 m; free-vehicle bottom setline; ANTON BRUUN cr. 16, sta. 618A; 25 May 1966.

DIAGNOSIS.—A large species (probably more than 100 cm) of *Coryphaenoides,* subgenus *Coryphaenoides,* with 1D. II,9–11, 1P. i18–i22, V. 8 (rarely 9). Teeth small, inconspicuous, bluntly pointed, in a single row in premaxillary, in one or two irregular rows on mandible. Snout blunt and completely scaled; terminal and lateral snout scutes weak or not developed. Suborbital region completely scaled, head ridges without enlarged modified scutelike scales.

COUNTS AND MEASUREMENTS (33 specimens).—D. II,9–11 + 95–111; 1P. i18–i22; V. 8 (9 in left fin of one spec.); GR-1 3–5 / (1–2) + 1 + (7–9) [9–11 total], GR-2 (0–1) + (0–1) + (2–8) [8–10 total] / (1–2) + (0–1) + (6–8) [8–11 total]; scales 1D. 8.5–11, 2D. 6.5–9.5, mid-1D. 5–7.5, lat.l. 34–44.

Total length 295+–810 mm; HL 63.0–183.5 mm. The following in percent HL: postrostral 73.3–79.4; snout 23.9–29.5; preoral 11.7–16.7;

FIGURE 17. *Coryphaenoides bulbiceps.* CAS 42518 (107.5 mm HL, 565 mm TL) from off Galapagos in 2,490 m.

internasal 16.5–20.5; interorbital 25.2–31.7; orbit 19.7–25.3; suborbital 12.1–16.6; postorbital 50.5–57.5; orbit–preop. 47.4–56.5; upper jaw 37.6–44.9; nostril 4.9–8.8; barbel 13.0–19.4; gill slit 9.9–15.4; pre-D. 106–125; pre-A. 163–187; pre-V. 96–116; V.–A. 58–89; isth.–A. 97–134; body depth 71–87; 1D.–2D. 13.4–55.3; 1D. 58–77; 1P. 48–80; V. 49–80.

DESCRIPTION.—Head broad, width about equal to depth behind orbits; length about 4.4–5.2 into TL. Body rather deep, greatest depth about equal to postrostral length of head, trunk long, distance isthmus to anal origin longer than HL, gradually tapering beyond vent; depth over anal origin about 0.6 of HL. Orbits moderate sized, about equal to snout and interorbital, about 2 into postorbital length. In adults, snout low, rather narrow, distance across lateral angles less than least interorbital width, bluntly rounded, scarcely protruding beyond large mouth; snout in young (UMML uncat.) more pointed and protruding. Scales on tip and lateral angles of snout not especially enlarged or scutelike. Interorbital space gently convex; orbits do not form part of dorsal profile. Mouth large, unrestricted at angles, rictus extends to below midorbit, maxilla to below hind ⅓ of orbit; lips thick, fleshy, papillaceous near teeth. Chin barbel slender distally, although rather stout at base; length about equal to least suborbital width. Suborbital region vertical in adults, smoothly rounded, without a sharp longitudinal ridge; in young, ridge forms a pronounced angle cross-sectionally. Preopercle large, slightly lobelike ventrally, hind margin almost vertical; preopercle ridge forms a slight lobe at posteroventral angle. Opercle-subopercle posterior margin smoothly curved; interopercle barely exposed as a naked tab at posterior tip.

Gill membranes attached to isthmus with no free fold, point of attachment slightly behind angle of lower jaw. Outer gill arch greatly restricted with a small outer slit, the length of which is less than least suborbital width. Gill rakers tubercular and weakly spined.

Sensory papillae on head numerous, distinctly dark colored, in contrast to paler ground.

Body and head covered with scales except for usual naked areas on lips, eyes, fins, nostrils, and gill membranes. No enlarged scutelike scales on head, although in large specimens (greater than

80 mm HL), scales on head ridges often stout and strongly adherent. Suborbital region divided into dorsal and ventral parts by differences in scales; those dorsally being slightly larger and coarser spinulated. Body scales covered with numerous rows of minute spinules that barely rise above horizontal; surface texture thus appears relatively smooth.

Teeth very small, tips barely protrude above thick gum matrix. Premaxillary teeth in 1 row; mandible teeth in 2 irregular rows, but 1 row laterally. Dentition in both jaws not occurring to posterior extent of rictus.

First dorsal fin moderately large; length second spinous ray about equal to postorbital length, denticulations along leading edge obsolescent or almost so, most of edge smooth; in small UMML specimens denticulations few, slender, weak, confined to distal half of ray. Second dorsal rudimentary throughout. Pectoral fin length about equal to postorbital length, posterior extent of fin well short of vertical through vent. Outer pelvic ray produced into a hairfine filament that just reaches vent, but falls short of anal origin. Anal well developed; origin behind that of second dorsal; vent region immediately in advance of fin without intervening scales.

Pyloric caeca of seven specimens long and slender, 9–16 total, longest caecum in one specimen (130 mm HL, CAS 42518) longer than postorbital length. Bends of intestine complex and variable (see Fig. 18). Swim bladder with tough external tunic, retia 4, long and slender; gas glands probably 4, but not accurately determined in few specimens examined for this.

Coloration in alcohol overall medium to light brown. Oral cavity pale to light gray; outer wall of gill cavity black, but inner wall medium brown; peritoneum black. Fins and nostril membranes dark brown to black; tips of anterior anal rays and first dorsal blackish. Lips, barbel, gular and most of branchiostegal membranes brownish gray; outer edge of branchiostegal membrane blackish.

DISTRIBUTION (Fig. 15).—Gulf of Panama, Cocos Ridge, Galapagos, in 1,710–3,193 m.

REMARKS AND COMPARISONS.—*Coryphaenoides bulbiceps* appears to be most closely related to *C. paradoxus* from the Pacific (and possibly also the Atlantic as *C. macrocephalus*—see Remarks in description of *C. paradoxus*), *C. thelostomus* Maul, 1951, and *C. longicirrhus* (Gilbert, 1905) from Hawaii. These four species attain a large size (more than 80 cm) and have the same general head physiognomy (low blunt snout, large subterminal mouth, suborbital region essentially vertical, without a distinct ridge, etc.). The minute teeth (uniserial [in adults, extra rows in young] in premaxilla, biserial in mandible) immediately distinguish the species from its closest congeners, and *C. paradoxus* and *C. longicirrhus* have more pelvic finrays (9–10 and 11, respectively). *Coryphaenoides thelostomus* further differs from *C. bulbiceps* in having smaller orbits (about 15% HL), shorter upper jaw (about 36–38%), longer pectoral fins (64–98%), longer pelvic fins (123–189%), and longer chin barbel (about 30–33%) (*C. thelostomus* data from Dooley 1979:541–542).

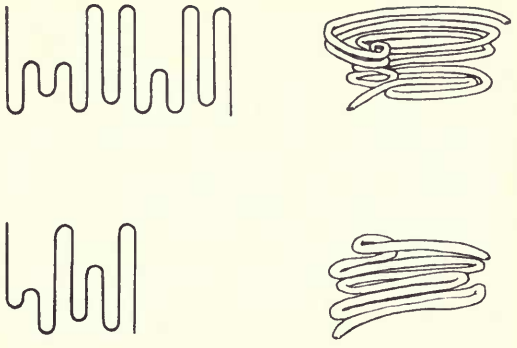


FIGURE 18. Diagrammatic exploded views of intestines of *Coryphaenoides bulbiceps*. (a) CAS 42518 (117 mm HL); (b) MMSU P-16518 (131 mm HL).

Coryphaenoides armatus, which has been captured at slightly greater depths in the same general region, differs notably in having a more pointed snout, smaller orbits, more pelvic fin rays (9–12), more retia (5–7), and extensive naked ventral areas on the snout and suborbital. Dentition and squamation features, among several other characters, readily distinguish *C. bulbiceps* from *C. bucephalus.*

Coryphaenoides bulbiceps has been taken and observed around thermal vent areas in the eastern Pacific (see Cohen and Haedrich 1983) and may very well be confined to areas harboring these geological features. Where found, adults of this large species appear to be numerous and have been noted to congregate around baited traps and cans within relatively short periods. They are susceptible to deep-set bottom longlines; 29 were captured on a pair of longline sets made by the research vessel ANTON BRUUN off the Ga-

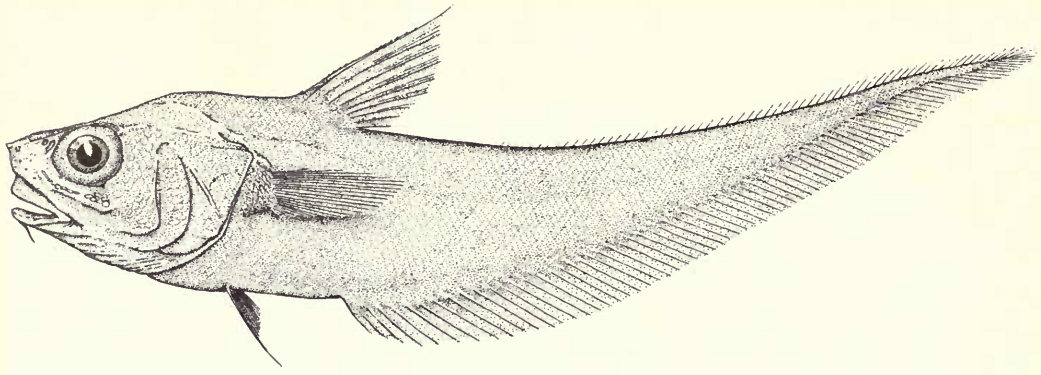


FIGURE 19. *Coryphaenoides capito.* CAS 55839 (57.1 mm HL) from off Ecuador in 945–960 m.

lapagos in 1966 (stations 618A, 618B). Cohen and Haedrich (1983) found the species to be the most abundant macrourid in their observations of Galapagos thermal vent communities (made from manned submersibles and time-lapse photography).

Coryphaenoides capito (Garman, 1899)

(Figures 4d, 19, 20)

Macrurus capito Garman, 1899:200–201 (type locality off Panama and Mexico).

?*Macrurus leucophaeus* Garman, 1899:201–202 (type locality off Panama). NEW SYNONYMY.

Macrurus vagrans Garman, 1899:201. NEW SYNONYMY.

MATERIAL EXAMINED.—Lectotype (here designated): MCZ 28591 (female: 37.0 mm HL, 140+ mm TL); 7°31′30″N, 79°14′W; 458 fm (935 m); ALBATROSS sta. 3384; 8 Mar. 1891. Paralectotypes: MCZ 63331 (1: 34.4 HL, 153+ TL); same data as for lectotype.—MCZ 28592 (5 paralectotypes, too deteriorated to measure) and USNM 12043 (1: ca. 30 HL, 114+ TL); 16°32′N, 99°48′W, 493 fm (902 m); ALBATROSS sta. 3417; 11 Apr. 1891.—MCZ 61093 (paralectotype of *Macrurus boops* Garman, 1899: 41.9 HL, 172+ TL); 7°21′N, 79°35′W; 511 fm (935 m); ALBATROSS sta. 3394; 10 Mar. 1891.—MCZ 28587 (paralectotype of *Macrurus boops*: 57.9 HL, 245+ TL); 7°09′30″N, 81°08′30″W, 546 fm (999 m); ALBATROSS sta. 3356; 23 Feb. 1891.—MCZ 28589 (holotype of *Macrurus leucophaeus* Garman, 1899; 47.2 HL, 185+ TL); 7°09′45″N, 80°50′W; 322 fm (589 m); ALBATROSS sta. 3354; 23 Feb. 1891.

Other material.—GULF OF CALIFORNIA.—SIO 68-83 (9: 36.3–77.4 HL, 152+–324+ TL); 27°40.0′N, 111°22.6′W; 40-ft otter trawl; THOMAS WASHINGTON, field no. MV68-I-50; 16 Jan. 1968. MEXICO.—CAS 55840 (6 of 29: 48.8–62.1 HL, 165+–245+ TL); 19°43.5′N, 105°35.5′W; 700–900 m; TE VEGA sta. 17; 10 July 1968.—CAS 55838 (1: 75.1 HL, 322 TL); 17°24′N, 101°31′W; 940–1,000 m; TE VEGA sta. 19; 12 July 1968. COSTA RICA.—CAS 43981 (2: 33.5–35.6 HL, 145+–135+ TL); off Cabo Blanco; 325–334 m; 14 Dec. 1975. PANAMA.—GCRL 14257 (1: 58.4 HL, 257+ TL); 7°13′00″N. 79°18′00″W; 305–841 m; M/V CANOPUS sta. 1291; 5 Mar. 1974. ECUADOR.—CAS 55839 (7: 45.8–68.0 HL, 175+–313+ TL) and ZMMU P-16518 (2 spec.); 3°15′S, 80°55′W; 945–960 m; ANTON BRUUN cr. 18B, sta. 770 (field no. LWK66-120); 10 Sep. 1966. PERU.—USNM 118019 (1: 66.1 HL, 304 TL); 5°47′S, 81°24′W; 536 fm (980 m); ALBATROSS sta. 4653; 12 Nov. 1904. NO LOCALITY.—MCZ 28583 (3: 24.9–31.1 HL, 87+–136+ TL); ALBATROSS 1888 Expedition.

DIAGNOSIS.—A species of *Coryphaenoides,* subgenus *Coryphaenoides,* with 1D. II,8–9; 1P. i19–i26; V. 8–9. Scales generally absent on lower portion of head including snout, anteriorly on suborbital, ventral margin of preopercle, most of interopercle, and most of lower jaw. Scales dorsally along suborbital ridge small but scutelike, slightly elongate, and in a single file; other more normal scales sometimes dorsal to this series in 1 or 2 rows and separated by a naked line of the sensory lateralis system. Leading margin of snout narrowly naked. All scales rather deciduous; spinules on scales weak, slender, short, arranged in irregularly parallel, longitudinal rows. Pyloric caeca stublike, 6–8, directed anteriorly. Vertical and horizontal arms of preopercular ridge form a right angle without a lobelike extension.

COUNTS AND MEASUREMENTS (34 specimens).—D. II,8–9 + about 95; 1P. i19–i26; V. 8–9; GR-1 5–9 / (1–2) + (0–1) + (10–12) [11–14 total]; GR-2 1 + (0–1) + (10–12) [total 11–13] / (1–2) + (0–1) + (7–10) [9–12 total]; scales 1D. 7–8 (17 spec.), 2D. 4.5–6.5 (14 spec.), mid-1D. 3.5–6.5 (15 spec.), lat.l. 31–38 (14 spec.); caeca 6–8 (8 spec.).

Total length 87+–324 mm; HL 24.9–77.4 mm. The following in percent of HL: postrostral 75.1–79.3; snout 22.3–28.4; preoral 10.0–17.1; internasal 11.4–15.7; interorbital 13.6–20.7; orbit 27.5–31.8; suborbital 7.1–11.3; postorbital 40.2–

49.9; orbit–preop. 31.0–35.6; upper jaw 26.9–32.2; nostril 4.1–6.9; barbel 5.4–10.2; gill slit 10.5–14.8; pre-D. 106–119; pre-A. 127–151; pre-V. 94–114; V.–A. 30–52; isth.–A. 60–86; body depth 60–89 (usually between 65 and 75); 1D.–2D. 18–59; 1D. 46–63; 1P. 47–60; V. 33–47.

DESCRIPTION.—Body and head relatively compressed, greatest head width in most adults about 0.6–0.7 greatest body depth, which in turn about equals postrostral length of head; HL 4.5–5.0 into TL. Supraoccipital crest high, forming pronounced hump in nape in all specimens and a dip in dorsal profile above orbits. Orbits large, 3.2–3.7 into HL, much longer than snout length; deeply incised into skull, resulting in narrow interorbital space (1.5–1.8 into orbit); orbit shape basically elliptical in young, becoming more ovoid in adults with narrow end anteroventral. Orbit margin anteroventrally fleshy in adults, not well defined by bony elements. Snout low, rather blunt, but armed with a single, small, conical scute at tip and 1 or 2 blunt scutes at lateral angles. Mouth opening restricted, rictus extends posteriorly to below anterior ¼ of orbits, premaxillary almost extends to vertical through midorbit. Barbel short, stout at base, but tapering to a fine tip. Suborbital ridge low, rounded, not sharply demarcated. Preopercle broadly rounded; chord of posterior margin essentially vertical; preopercular ridge low, no lobelike extension of ridge at posteroventral angle (as in *C. anguliceps* and *C. ariommus*). Opercle, subopercle, and interopercle broadly exposed, their free margins smoothly adjoined without deep incisions or lobes.

Gill membranes thick, broadly attached to isthmus, without a free posterior fold; gill openings on each side completely separate. Gill rakers tubercular, those on second and third arches armed with several long sharp spines.

Scales cover most of dorsal surfaces of head, but broad naked areas on ventral surfaces of snout and suborbital, mandibular rami, and lower margins of opercle and interopercle. Naked ventral surfaces of snout extend onto leading upper edge (except for terminal and lateral scutes) of snout. Boundaries of postorbital sensory canals and most edges of opercular bones narrowly naked. Interopercle sparsely scaled in middle portion of exposed surfaces. Areas around nostrils, orbital rim between nostrils and eye, suborbital ridge, and lower (horizontal) preopercle ridge naked. Only a single row of small, elongated, deeply embedded scales along anterior half of suborbital shelf. A cluster of small scales present below nostrils. Gill membranes naked. Body scales (Fig. 4d) rather large, highly deciduous (as are most head scales), covered with short, sharp, conical spinules arranged in generally parallel longitudinal rows (5–8 rows in larger scales below 1D.–2D. interspace). A row of small scales proximally on shank of second spinous ray; other small scales proximally on membranes of first dorsal fin rays.

Jaw teeth very small, slender, sharp, conical, deeply embedded within fleshy gum matrix; arranged in narrow, gradually tapered bands (2–4 teeth wide at broadest point) on mandibles, in moderately broad bands (6–7 teeth wide) on premaxillaries; no teeth significantly enlarged.

First dorsal relatively low, greatest height much less than postrostral length of head, base rather steeply inclined; first spinous ray a short splint closely appressed to base of stout, tapered second spinous ray, which has a finely serrated leading edge and filamentous tip. Second dorsal poorly developed throughout; origin poorly defined in larger individuals where anteriormost rays not developed, although pterygiophores present. Pectorals broad, well developed, extend to above sixth to eighth anal ray. Pelvic fins small, origin far forward below opercle; outermost ray thin, hairfine at tip, barely reaches vent. Anal origin below, or slightly behind vertical of, posterior edge of first dorsal.

Coloration in alcohol, SIO 68-83 specimens from Mexico swarthy; faint violet tinge on head; fin rays of first dorsal, pectoral, and pelvics swarthy to black. Other specimens examined paler, brownish; scaleless and abraded surfaces whitish. Oral and gill cavities blackish.

DISTRIBUTION (Fig. 20).—Mainland Mexico into Gulf of California and south to northern Peru, 305–1,000 m.

REMARKS AND COMPARISONS.—Relationships of *C. capito* to *C. boops* have been discussed under the latter species. Specimens larger than about 50 mm HL are most likely to be confused with the sympatric *C. anguliceps,* but the two are immediately distinguishable by the shape of their preopercular ridge, which forms a right angle with no lobe in *C. capito* versus an acute angle with a pronounced lobe in *C. anguliceps.* Counts of gill rakers, pyloric caeca, and lateral line scale rows (over distance equal to predorsal length) also differ notably between the two species.

The five syntypes (MCZ 28592) from ALBATROSS sta. 3417 are all in such poor con-

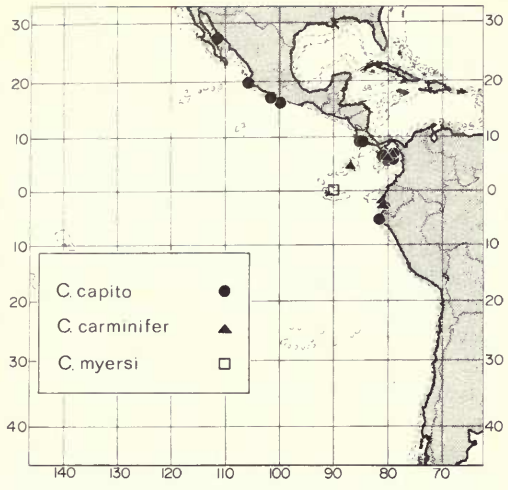


FIGURE 20. Map showing distributions of *Coryphaenoides capito, C. carminifer,* and *C. myersi.*

dition that counts and measurements could not be made. These syntypes were called *Macrurus vagrans* by Garman in his original description of *C. capito*: "The specimens from Station 3417 are hardly identical in variety with those from Station 3384; they are closely allied but differ in that the former (*M. vagrans*) is darker in color, and has less of the silver tint." (Garman 1899:201). This brief passage could be construed as an original description of the variety "*vagrans*" of *Macrurus capito,* and the International Code of Zoological Nomenclature (1985 ed., Art. 45(g)(ii)) states that "a new name published expressly for a "variety" or "form" . . . is: . . . subspecific if published before 1961." Thus, based on the Code, the name *vagrans* is to be treated as a subspecific taxon of *M. capito.* One of us (TI) examined the specimens and found them somewhat different in scale features from that of the other type series. In general, the scales had fewer spinules, and in some areas (behind 1D.; over pelvic fins; on belly) the scales entirely lacked spinules. Most spinuleless scales had about three low ridges, although those on the belly had none. These slight differences between "*Macrurus vagrans*" and *Macrurus capito* do not seem sufficient to warrant recognition of *M. vagrans* as either a distinct species or a subspecies, although more material from the type locality may suggest otherwise.

We have questionably placed *Macrurus leucophaeus* Garman, 1899, into the synonymy of *C. capito* because there appeared to be no significant feature that would differentiate the holotype (and only specimen) from *C. capito.* Minor differences in squamation were, however, found. The holotype had a row of elongate, thickened nonimbricate scales along the suborbital ridge similar to that found in *C. capito,* but there were also two additional rows of more normal scales dorsally separated from the first row by the cephalic lateral line system. These rows of more normal scales extend forward to cover most of the area below the suborbital ridge, the scales extend forward in a narrow line to below the anterior rim of the orbits, but the snout ventrally is naked.

Coryphaenoides carminifer (Garman, 1899)

(Figures 3b, 20–22)

Macrurus carminifer (Garman, 1899:204–206, pl. 46, fig. 2 (type locality: Gulf of Panama, 1,020 fm [1,865 m], ALBATROSS sta. 2393; other type specimens from ALBATROSS sta. 3353, 3354, 3395, in 584–1,335 m).

Coryphaenoides carminatus: Gilbert and Hubbs 1916:143 (misspelling of *C. carminifer*; list).

Coryphaenoides carminifer: Makushok 1967:221 (table).

MATERIAL EXAMINED.—Holotype: MCZ 28582 (53.7 mm HL, 295 mm TL); Gulf of Panama, 7°15′N, 79°36′W; 1,020 fm (1,865 m); ALBATROSS sta. 3393; 10 Mar. 1891. Paratype: USNM 57860 (1: 55.8 HL, 290+ TL); 7°06′15″N, 80°34′W; 695 fm (1,271 m); ALBATROSS sta. 3353; 23 Feb. 1891.

Other material.—COCOS I. (96 km S of).—AMNH 7513 (1: 63.7 HL, 325+ TL); ARCTURUS sta. 74. ECUADOR.—CAS 42519 (3: 47.5–55.5 HL, 248+–298+ TL); 2°20′S, 81°16′W; 850–1,400 m; TE VEGA cr. 19, sta. 84; 4 Aug. 1968.—CAS 56109 (2: 47.5–52.1 HL, 258+–260+ TL); 2°25′S, 81°10′W; 700–1,000 m; TE VEGA cr. 19, sta. 148; 1 Sep. 1968.—CAS 56101 (5: 28.6–72.9 HL, 144+–355+ TL) and MMSU P-16519 (2: 46.0–51.0 HL, 247+–262+ TL); 3°15′S, 80°55′W, 945–960 m; ANTON BRUUN cr. 18B, sta. 770 (field no. LWK66-120; 10 Sep. 1966.

DIAGNOSIS.—A species of *Coryphaenoides,* subgenus *Coryphaenoides,* with chin barbel thick, about 0.5–0.8 orbit diameter; 1D. II,8–10; 1P. i18–i21; V. 8–9 (usually 8); mouth opening restricted, rictus scarcely extending to vertical through anterior orbit margin; teeth uniformly small on both jaws, in narrow bands; snout short, blunt, protruding little beyond mouth; body and head uniformly scaled, without naked areas on snout, suborbital, or preopercle, and mandibles mostly scaled; scales densely covered with sharp, reclined, spikelike to somewhat lanceolate spinules in discrete parallel rows; outer pelvic ray thick and prolonged; second spinous ray of 1D. heavy and triangular in cross section basally, rap-

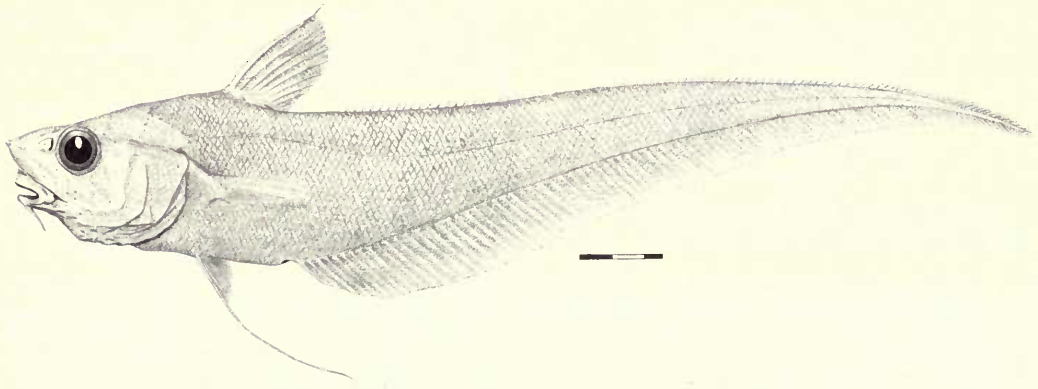


FIGURE 21. *Coryphaenoides carminifer*. CAS 42519 (47.5 mm HL) from off Ecuador in 850–1,400 m.

idly tapering to filamentous tip, leading edge serrated distally, but serrations become obsolete basally; preopercle broadly rounded, not lobed; preopercle ridge not forming lobes at angle; posterior tip of interopercle exposed and scaled.

COUNTS AND MEASUREMENTS (17 specimens).—1D. II,8–10, 1P. i16–i22 (usually i19–i21); V. 8–9; A. and 2D. about 100–110; GR-1 (3–6) / (1–2) + (0–1) + (8–9) [8–10 total], GR-2 (1–2) + (0–1) + (6–7) [total 8–10] / (1–2) + (0–1) + (6–7) [8–9 total]; scales 1D. 9–12, 2D. 7–9.5, mid-1D. 5.5–8.5, lat.l. 37–44; caeca 8 or 9.

Total length 144+–355+ mm; HL 28.6–72.9 mm. The following in percent of HL: postrostral 72.8–76.8; snout 26.1–30.6; preoral 13.6–17.5; internasal 21.7–24.8; interorbital 26.1–31.3; orbit 25.9–31.1; suborbital 11.9–14.7; postorbital 42.3–46.9; orbit–preop. 34.4–38.1 (41.3); upper jaw 26.7–32.0; nostril 5.1–9.3; rictus 18.6–20.4; barbel 13.7–23.4; gill slit 4.1–8.1; pre-D. 108–124; pre-A. 139–171; pre-V. 105–124; V.–A. 40–60; isth.–A. 78–94; body depth 80–93; 1D.–2D. 23.4–48.0; 1D. 72–84; 1P. 51–66; V. 78–117.

DESCRIPTION.—Head and body moderately compressed, greatest width over pectoral bases about half greatest body depth, HL 4.0–5.0 into TL. Orbits round, about equal to interorbital width and to snout length. Interorbital space slightly depressed to almost level. Snout short, bluntly pointed, extending little beyond mouth. Mouth opening restricted posterolaterally by lip folds; rictus about ⅔ length upper jaw, end of rictus below anterior edge of orbit; maxilla terminates below anterior ⅓ of orbits. Barbel notably stout, thickened over most of length; abruptly tapered to a fine tip, length 0.52–0.80 orbit diameter. Suborbital region smoothly rounded in well-preserved specimens, the shelf region broad, not sharply narrowed anteriorly. Preopercle broadly rounded, not lobed, posterior margin nearly vertical; preopercle ridge forming a moderate lobe at angle. Posterior margin of gill cover steeply inclined from posterodorsal angle, gently curved at ventral edge of subopercle, where interopercle protrudes broadly beyond preopercle.

Gill membranes thick, broadly attached to isthmus, without a free posterior fold. First gill arch broadly attached to gill cover by folds of skin. Outermost gill slit greatly restricted, length less than that of longest gill filament. Second slit unrestricted; third and fourth restricted at ventral end by folds of skin; fifth slit restricted dorsally and ventrally but wider than first slit. Ceratobranchial gill rakers tubercular, tipped with small spines; epibranchial rakers platelike, broadly triangular, with tufts of spines of various lengths. Gill filaments of moderate length, but substantially less than least suborbital width.

Scales evenly cover all of body and head except for fins, gill membranes, nostril membranes and adjoining orbital rim, and anterior end of mandibular rami. Scales (Fig. 3b) large, adherent, densely covered with parallel longitudinal rows of slender, lanceolate, reclined spinules, about 13–14 rows in large scales below dorsal fins in a specimen 72.9 mm HL, 8–9 rows in a specimen 48 mm HL. Small scales at base of rays of first dorsal and pelvic fins. A few small scales on exposed tip of interopercle. A stout, spiny, tubercular scale at snout tip, and one or more blunter ones at lateral angles. Scales on suborbital shelf

FIGURE 22. Right lateral view of intestines of *Coryphaenoides carminifer*, CAS 56101 (46.3 mm HL).

not notably different from adjacent scales. Head ridges not armed with stout scutelike scales.

Narrow bands of small, sharp, strongly recurved teeth on both upper and lower jaws; the dentary bands about 3 teeth wide near symphysis, the premaxillary bands about 4 teeth wide. No teeth enlarged. Bands extend posteriorly to end of rictus, but not much, if at all, beyond.

Height of first dorsal about equal to postrostral length of head. Second spinous ray stout and triangular in cross section at base, tapering rapidly to a fine tip; sharp leading edge with small sawtooth serrations distally, but obsolescent proximally, even in smallest specimens examined. Second dorsal rudimentary throughout. Pectorals broad, extend to above anal fin origin. Pelvics small except for thick, greatly elongated outer ray, which extends to about the 9th–13th anal ray; other rays fall well short of anal origin. Anal fin well developed, origin behind vertical through hind edge of first dorsal fin. Pectoral origin slightly in advance of pelvic origin, which in turn slightly precedes that of first dorsal.

Cephalic sensory canal system well developed, particularly on ventral surfaces of head and dorsally on snout and interorbital region. System represented by series of low papillae, but no large open pores.

Alimentary canal long, multiply looped (see Fig. 22); pyloric caeca long, slender, longest caecum about equal to interorbital width, 8 and 9 in 2 specimens. Swim bladder large, filled with fatty tissue; 4 globular gas glands connected to 4 slender retia in CAS 42519 (55.5 mm HL), but gas glands in CAS 56101 (46.3 mm HL) in flattened coalesced mass without distinct separations. Males have large drumming muscles anteroventrally on swim bladder.

Coloration in alcohol dark brown overall; fins blackish, although elongated pelvic ray white. Gill membranes pale brown in some, blackish in others. Oral cavity light grayish to pale. Lips dark brown around mouth opening; other skin folds around mouth pale brown. Chin barbel light brown. Gill chamber dark gray to blackish; peritoneum blackish or dark brown.

DISTRIBUTION (Fig. 20).—Gulf of Panama (Panama) to Gulf of Guayaquil (Ecuador) in 589–1,865 m.

REMARKS AND COMPARISONS.—*Coryphaenoides carminifer* appears to be in the *C. boops-capito-myersi* species complex discussed in the description of *C. boops*. *Coryphaenoides carminifer* differs from the other three in having a much thicker chin barbel, a posteriorly prolonged preopercle-ridge angle, and a somewhat higher, more protruding snout. It further differs from *C. capito* and *C. boops* (but not *C. myersi*) in having a thick, elongated outer pelvic ray and long slender pyloric caeca. In its thick barbel, *C. carminifer* resembles *C. zaniophorus* Vaillant, 1888, from the Atlantic, but it differs from that species in having gill openings less far forward (under posterior margin of orbit in *C. zaniophorus*); more pointed, protruding snout; fewer pelvic rays (usually 10, sometimes 9 in *C. zaniophorus*); and fewer gill rakers (11–12 total on second arch in *C. zaniophorus*).

Coryphaenoides delsolari Chirichigno and Iwamoto, 1977

(Figures 3d, 23, 24)

Coryphaenoides delsolari Chirichigno and Iwamoto, 1977:519–528 (type locality: Ecuador, ANTON BRUUN sta. 770 in 945–960 m). Parin and Sazonov 1983:86 (7 spec.; 3 localities off Peru; 600–610 m).

Nematonurus sp. aff. *altipinnis:* Chirichigno 1968:418–421, fig. 13 (descr., illus.); 1969:37, fig. 81 (list).

Coryphaenoides nov. sp. Chirichigno, 1974:315, fig. 622–624 (in key).

The description given here is an abridgement of the extensive original by Chirichigno and Iwamoto (1977).

MATERIAL EXAMINED.—Type specimens (examined by TI); others from off Peru (examined by VIS): MMSU P-16523 (6: 32.5–81 HL, 158–365 TL); 7°41'S, 80°40'W; 900–1,000 m; IKMT on bottom at 900 m; AKADEMIK KURCHATOV sta. 1472; 4 Mar. 1972.—MMSU P-16524 (3 spec.); PROF. MESIATZEV trawl 44.—MMSU P-16525 (3 spec.); PROF. MESIATZEV trawl 45.—MMSU P-16526 (1 spec.); PROF. MESIATZEV trawl 66.

DIAGNOSIS.—A species of *Coryphaenoides* with head and body scales densely covered with fine, relatively erect spinules, most with multipronged, usually tridentate tips in adult specimens larger than 50 mm HL. Head and body completely and uniformly scaled except for naked exposed tip of interopercle. 1D. II,8–11 (usually II,8–9); V. 9–10 (rarely 11). Inner gill rakers

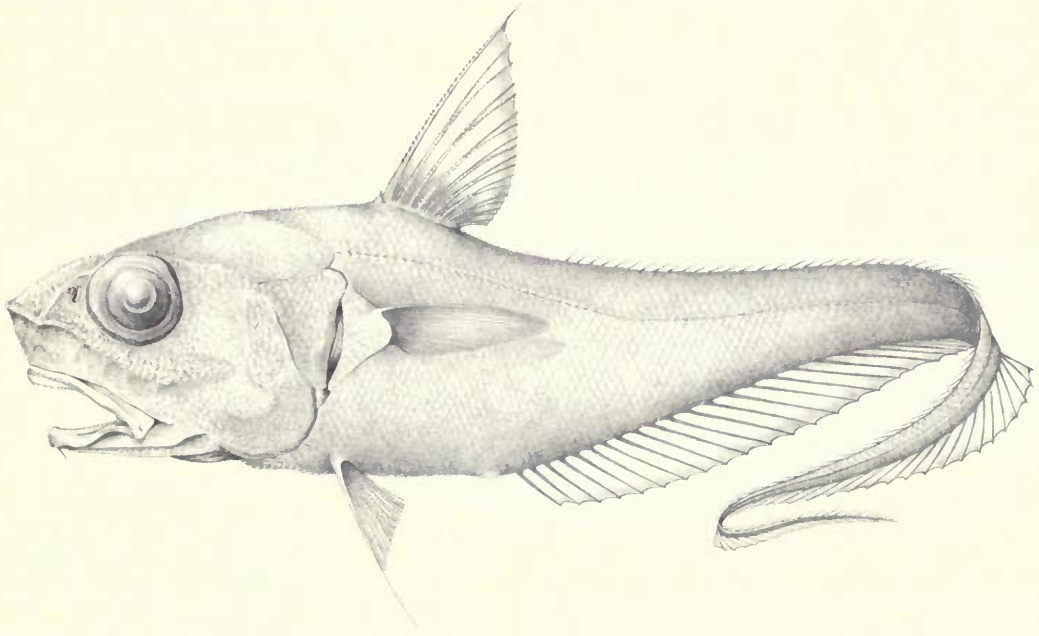


FIGURE 23. *Coryphaenoides delsolari.* Drawing of holotype (USNM 215278) from Chirichigno and Iwamoto (1977, fig. 1).

on first arch 1–2 + 9–11 (10–13 total); inner rakers on second arch 1–2 + 9–11 (10–13 total). Snout blunt, high, scarcely protruding. Upper jaw 2.4–2.9 in head; orbits 2.9–3.4. Barbel short and thin, usually 4 or more into orbit. Teeth small, in moderately broad band in upper jaw with outer series slightly enlarged; in narrow band on lower jaw.

COUNTS AND MEASUREMENTS.—1D. II,8–10 (rarely 11); 1P. (i18)i19–i23; V. 9–10(11); GR-1 (5–7) / (1–2) + (9–12) [total 11–14], GR-2 ? / (1–2) + (9–11) [10–13 total]; scales 1D. 8–12, 2D. 6–9, mid-1D. 4.5–8, lat.l. 30–34; vert. 12; caeca 11–14.

Measurements in percent of HL: postrostral 70–79; snout 26–32; preoral 13–24; internasal 20–25; interorbital 23–32; orbit 23–34; suborbital 12–17; postorbital 38–50; orbit-preop. 42–50; upper jaw 35–41; barbel 3–10; gill slit 11–17; pre-A. 128–164; V.–A. 28–53; isth.–A. 60–91; body depth 58–87; 1D.–2D. 13–45; 1D. 50–66; 1P. 53–67; V. 38–57.

DESCRIPTION.—Head large, deep, broad in juveniles, more compressed in adults. Snout pointed in juveniles, blunt in adults; lateral profile arched. Interorbital space somewhat concave, width less than orbit diameter in young, but more in large adults. Suborbital region broad, with a stout dorsal shelf of scutelike scales. Preopercle ridge produced into a narrow lobe posteroventrally; preopercle margin forms a broad lobe. Interopercle exposed as a narrow triangle posteriorly. Mouth large, maxillary extends to below posterior half of orbit; rictus little restricted. Barbel short, thin, only slightly longer than diameter of posterior nostril. Opercular openings wide, but membranes rather broadly attached to isthmus.

Height 1D. less than postrostral length of head; the second spinous ray finely serrated, slightly produced. Outer pelvic ray slightly produced, its filamentous tip extends little beyond anal origin. Origins of 1D. and 1P. about on same vertical, that of V. a bit anterior.

Dentition generally small, teeth in upper jaw arranged in a broad band with a slightly enlarged outer series, those in lower jaw in a narrow band.

Almost all of head and body uniformly scaled including most of ventral aspects of snout and suborbital (ventral margin narrowly naked, however), and lower jaw rami. Scales of trunk and tail densely covered with slender, relatively erect spinules arranged in irregularly divergent rows.

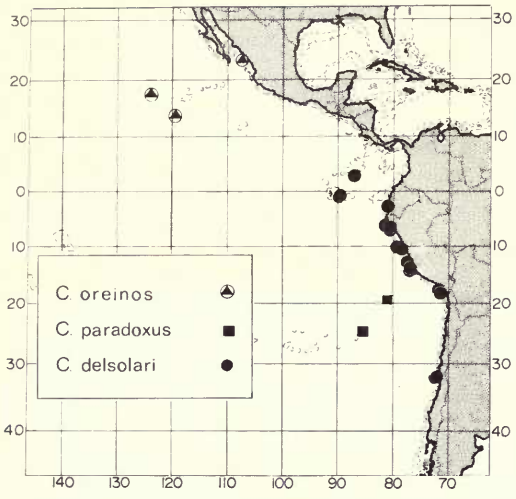


FIGURE 24. Map showing eastern Pacific distributions of *Coryphaenoides delsolari, C. paradoxus,* and *C. oreinos.*

In specimens larger than about 80 mm HL, most scales have narrow lanceolate spinules with tridentate or multipronged tips. In specimens 50–80 mm HL, tridentate spinules variously developed. In smaller specimens, spinules few, conical, and with slender recurved tips.

Large swim bladder with 4 long slender retia, each connected to a small peltate gas gland. Pyloric caeca short, rather thick, simple.

Color in alcohol generally dark brown in adults, paler in young, with brownish black fins, gill membranes, and lips. Linings of mouth, gill, and abdominal cavities blackish.

DISTRIBUTION (Fig. 24).—Cocos Ridge, Galapagos, Ecuador, Peru, to central Chile (32°S), in 580–1,200 m.

REMARKS AND COMPARISONS.—*Coryphaenoides delsolari* is apparently closest to the western Pacific *C. altipinnis* Günther, 1877, but the latter species has a longer barbel, narrower suborbital, larger posterior nostril, and different scales. Of the eastern Pacific species, *C. delsolari* is readily distinguished from *C. bucephalus* by its much smaller teeth, higher gill raker count (9–10 in *bucephalus*), shorter barbel, longer outer gill slit, and different scale spinules. It differs from *C. bulbiceps* in its fewer pelvic fin rays; narrower internasal; somewhat smaller orbits; a longer postorbital length; longer barbel; longer preanal, outer V. to A., and isthmus to A. distances; and scale spinulation. The combination of scale spinules, mouth size, length outer gill slit, pelvic fin ray count, barbel size, and dentition distinguish *C. delsolari* from all other congeners.

Coryphaenoides oreinos n. sp.

(Figures 3e, 24–26)

Macrurus bucephalus Garman, 1899 (partim; specimen from ALBATROSS sta. 3430).

HOLOTYPE. NSMT P44088 (formerly FSFL NA-280) (80.5 mm HL, 413 mm TL); Dowd Tablemount off Mexico; 13°27.5′N, 119°54.8′W; 1,200–1,626 m; KAIYO MARU sta. LL7; multiple-hook setline; 9 Feb. 1979.

PARATYPES. FSFL NA-281 (1: 93.5 HL, 444+ TL) and NSMT P44080 (formerly FSFL NA-282) (1: 85.5 HL, 405 TL), same data as for holotype.—FSFL NA-349 (1: 132 HL, 650+ TL); Seamount 375 off Mexico, 17°40.9′N, 124°02.5′W; 990–1,100 m; KAIYO MARU sta. LL12; multiple-hook setline; 18 Feb. 1979.—MCZ 28600 (1: 46.4 HL, about 220 TL); Mexico off Mazatlan; 23°16′N, 107°31′W; 852 fm [1,558 m]; ALBATROSS sta. 3430; 19 Apr. 1891 (paralectotype of *Macrurus bucephalus* Garman, 1899).

DIAGNOSIS.—A species of *Coryphaenoides,* subgenus *Coryphaenoides,* with 1D. II,8–10, V. 9–10. Snout broad, rounded, naked except for 2 spiny tubercular scales at lateral angles, a series of small coarse scales along posterior portion of median nasal ridge, and a wedge of small scales intruding forward from interorbital region on each side of median ridge. Naked margins on head bones prominent. Spinules on scales reduced, lacking along outer scale margins, about 8–12 subparallel ridges, few with sharp spinules. Teeth small in broad bands in both jaws. Internasal width about 5 in head, interorbital about 4, slightly greater than orbit diameter; barbel small, about 0.5 or less into orbit; upper jaw 36–39% HL.

COUNTS AND MEASUREMENTS (5 specimens; see also Table 2).—1D. II,8–10; 1P. i19–i26; V. 9–10; GR-1 0–4 / (1–2) + (7–9) [9–11 total], GR-2 (1–2) + (7–8) [8–10 total] / 2 + (7–8) [9–10 total]; scales 1D. 6.5–8, 2D. 6.5–9.5, mid-D. 6.5–8, lat.l. 45–49.

Total length about 220–650+ mm; HL 46.4–132 mm. The following in percent HL; postrostral 75.0–77.4; snout 25.0–27.8; preoral 12.9–19.6; internasal 19.4–21.7; interorbital 23.4–26.4; orbit 21.6–24.7; suborbital 13.2–15.9; postorbital 50.6–56.4; orbit–preop. 47.7–50.1; upper jaw 36.0–39.0; nostril 3.2–6.1; barbel 8.8–10.8; gill slit 8.5–10.3; pre-D. 105–116; pre-V. 109–119; pre-A. 142–159; V.–A. 35–52; isth.–A. 69–89; body depth 74–86; 1D.–2D. 21–32; 1D. 53–67; 1P. 48–55; V. 43–60.

DESCRIPTION OF HOLOTYPE.—Head laterally

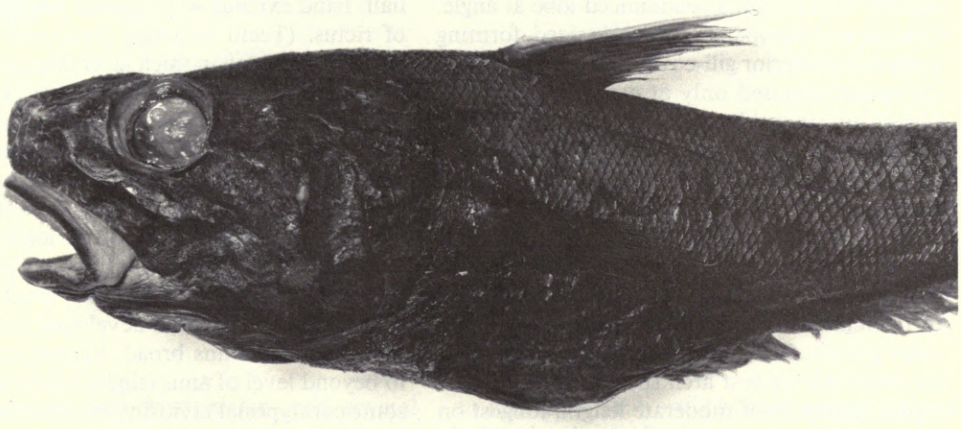


FIGURE 25. *Coryphaenoides oreinos* Iwamoto and Sazonov, new species. Holotype, NSMT P44088 (80.5 mm HL, 413 mm TL) off 950 Dowd Tablemount off Mexico in 1,200–1,626 m.

compressed, width about equal to greatest depth of opercular region; length more than 5 in TL. Trunk moderate, distance isthmus to anal almost as long as HL. Anus immediately adjacent to anal fin origin. Snout blunt, high, scarcely protruding beyond mouth; dorsal profile little elevated. Orbits round, relatively small, diameter much less than snout length, slightly less than interorbital space. Interorbital relatively flat, about 4 into HL. Mouth of moderate size, rictus extends posteriorly to below anterior ¼ of orbits; maxillary to below midorbit (or slightly beyond). Barbel

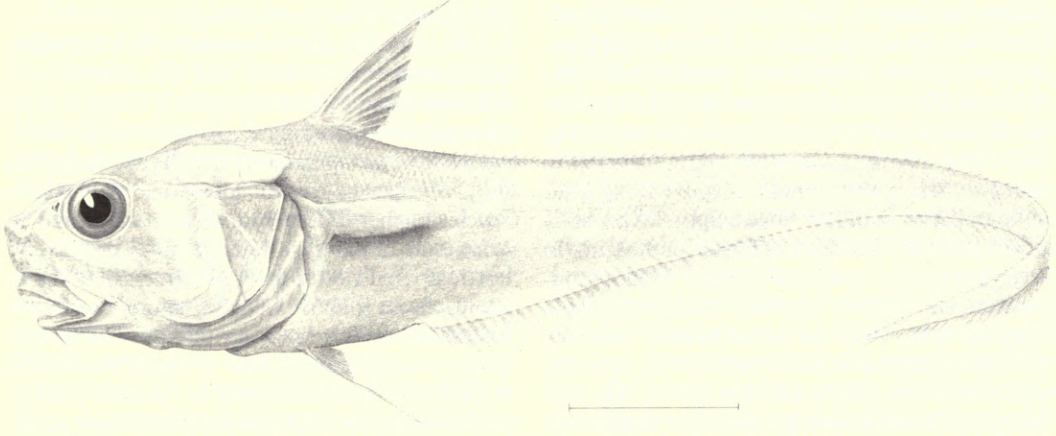


FIGURE 26. *Coryphaenoides oreinos* Iwamoto and Sazonov, new species. Paratype, MCZ 28600 (46.4 mm HL) from off Mazatlan, Mexico in 1,558 m (fins, scales, and parts of trunk and tail reconstructed). Scale bar equals 25 mm.

short and thin. Suborbital region broad, not sharply angular, the upper shelf area gently rounded, without strong spiny ridges. Preopercle large, posterior margin slightly inclined from vertical, with a broad rounded angle; the preopercle ridges form a pronounced lobe at angle. Opercle and subopercle moderate sized, forming a smooth posterior gill-cover margin. Interopercle naked, exposed only at extreme tip, which blends in smoothly with subopercle. Nostrils small, about 3 into suborbital width. Sensory papillae of head well developed, especially on snout, suborbital, and mandible.

Gill membranes narrowly attached to isthmus, opposite sides joined below vertical arm of preopercular ridge. Outer gill arch broadly restricted to operculum by folds of skin, leaving a small outer gill slit. Gill rakers small, tubercular, none on outer side of first arch (but present in paratypes); filaments of moderate length, longest on first arch about equal in length to outer gill slit.

Scales (Fig. 4e, f) small, uniformly cover all of trunk and tail except fins. Head mostly covered except on snout, suborbital, lower jaw, interopercle, margins and ridges of preopercle, and margins of opercle, parietal, and orbits. Scales on suborbital confined to a narrow wedge of small scales intruding forward from preopercle to below anterior edge of orbits; those on mandible limited to a medial row or 2 on posterior half of ramus. All ventral surfaces of snout naked except for small scutes at lateral snout angles; these scutes armed with stout conical posteriorly directed spinules. Terminal scute absent. A series of 6 small but relatively stout scales on posterior half of median nasal ridge; similar scales along dorsal border of orbits (these extend forward to over posterior end of supranarial ridges in larger paratypes). A patch of apparently regenerated scales between 2D. origin and lateral line having a single series of spinules along posterior edge (Fig. 4f). These aberrant scales have small conical to narrowly triangular spinules aligned along 8–12 subparallel rows of low ridges. Spinules on body scales generally fall short of posterior margin. (In large paratypes, posterior margin broadly spinuleless, the spinules confined to anterior part of exposed field.) A broad naked area around 1D. base; thin spinuleless scales behind 1D., pectoral, and pelvic fins. Belly between pelvic fins and margin of isthmus and gill chamber edged with similar scales.

Teeth on premaxillary small, in moderately broad tapered bands about 7–8 teeth wide, the bands extending almost to end of rictus; outer series of stout, enlarged, conical, slightly recurved teeth. Mandibular teeth small, in narrow band 2–5 teeth wide, broadest along posterior half; band extends well beyond posterior extent of rictus. (Teeth in larger paratypes generally deeply embedded in thick layer of gum papillae.)

First dorsal fin rather short, length about equal to postrostral length; second spinous ray serrated, filamentous at tip but not produced beyond first 2 segmented rays; a low keellike process developed at base on spine (not present in paratypes; in larger paratypes distal teeth on spine long and tightly appressed, almost coalesced). Second dorsal fin rudimentary anteriorly, becoming moderately well developed towards end of tail. Pectoral fins broad, longest rays extend to beyond level of anus (slightly short of anus in some paratypes). Pelvic fins moderate sized, outermost ray much thicker than others and prolonged into a hairfine tip that extends to base of fourth anal ray; other rays fall well short of anus. First dorsal and pectoral fins about on same vertical; pelvic fin origin slightly anterior to that vertical.

Color in alcohol dark chocolate brown overall, fins black. Oral cavity gray, gill cavity lining and peritoneum blackish. Barbel pale. Branchiostegal membranes black. Gill arches, rakers, and filaments pale.

Distribution (Fig. 24).—Seamounts off central Mexico in 990–1,626 m.

Etymology.—From the Greek *oreinos* (from the mountains, mountain dwelling), in reference to the habitat of the new species on seamounts and guyots of the eastern Pacific.

Remarks and Comparisons.—The extensive naked areas on the head and the absence of a terminal snout scute distinguish *C. oreinos* from all congeners including *C. bucephalus, C. bulbiceps,* and *C. paradoxus,* the eastern Pacific species most similar in overall appearance. The new species further differs from *C. anguliceps* and *C. ariommus* in having a blunter snout profile and less restricted rictus; from *C. myersi* in a higher snout, fewer pelvic fin rays, more deciduous scales, and weaker scale spinulation. The species bears some resemblance to *Coryphaenoides* (*Chalinura*) *fernandezianus* in its blunt snout, naked regions on head, and thin, deciduous scales, but it differs in having larger orbits, mandibular teeth in a band (versus in one row), shorter upper

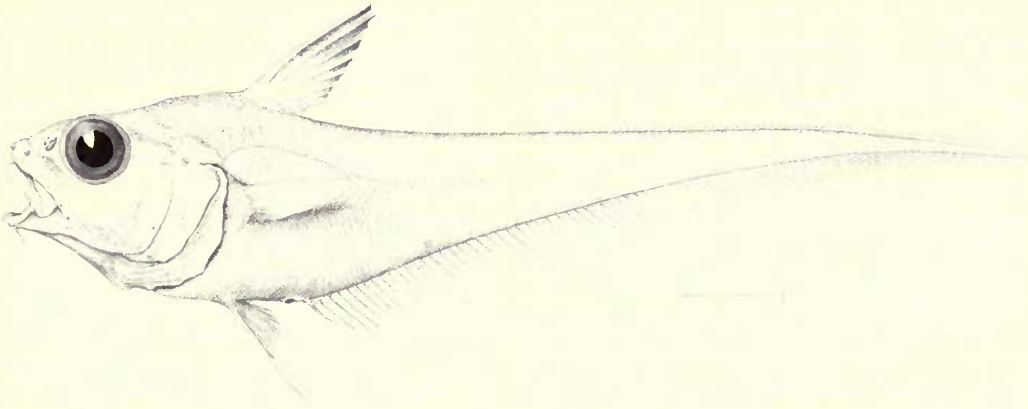


FIGURE 27. *Coryphaenoides myersi* Iwamoto and Sazonov, new species. Holotype, CAS 56103 (55.0 mm HL) from Galapagos in 457 m.

jaws, narrower suborbital region, and several other features. In many squamation features it resembles members of the subgenus *Chalinura,* but differs in lacking scales along the leading edge of the snout, and has different mandibular dentition and interopercle shape. Other eastern Pacific *Coryphaenoides* differ widely from the new species, and possibly its closest relationships lie with western Pacific or Indian Ocean species.

Coryphaenoides myersi n. sp.

(Figures 4e, 20, 27)

HOLOTYPE.—CAS 56103 (55.0 mm HL, 262+ mm TL, incomplete, a small pseudocaudal developed); 1°09'S, 90°35'W; 250 fm [457 m]; collector G. S. Myers, VELERO sta. 802-38; 23 Jan. 1938.

DIAGNOSIS.—A species of *Coryphaenoides,* subgenus *Coryphaenoides,* with 1D. II,9, 1P. i24, V. 10; outer pelvic ray elongated and thick. Snout low, scarcely protruding, preoral length 8% HL. Underside of snout, most of mandibular rami naked, scales otherwise uniformly cover head and body; spinules long, conical, densely packed in parallel to convergent rows. Orbits large, 3 into HL, twice interorbital space. Teeth small, in bands in both jaws; none in premaxillary enlarged. Mouth small, upper jaws about 3 in HL; rictus does not extend beyond level of posterior nostril. Barbel small, more than 3 into orbit.

COUNTS AND MEASUREMENTS.—D. II,9 + 70+; A. 81+; 1P. i24/i24; V. 10/10; GR-1 5 / 2 + 1 + 8, GR-2 1 + 0 + 8 / 1 + 1 + 7; scales 1D. 10.5, 2D. 8.5, mid-1D. 8 (excluding those on fin), lat.l. 38; vert. 11; anal pterygiophores before first haemal spine 7.

Measurements in mm followed by percent HL in parentheses; postrostral 42.1 (76.6); snout 14.7 (26.7); preoral 4.3 (7.8); internasal 7.7 (14.0); interorbital 9.7 (17.6); orbit 19.0 (34.5); suborbital 7.0 (12.7); postorbital 22.9 (41.6); orbit–preop. 17.5 (31.8); upper jaw 17.7 (32.2); rictus 12.8 (23.3); nostril 3.9 (7.1); barbel 5.1 (9.3); gill slit 5.8 (10.5); pre-D. 62 (113); pre-A. 86 (156); pre-V. 67.5 (123); isth.–A. 40 (72.7); V.–A. 20.8 (37.8); body depth 52 (95); depth over A. origin 47 (86); 1D.–2D. 29 (53); 1P. 34.5 (63); V. 34 (62); 1D. base 13 (24).

DESCRIPTION.—Body compressed, deep, greatest depth under first dorsal origin about equal to head length; body tapers rapidly from anal origin to tip of tail. Head 4.7 in TL, but tail incomplete, probably about 5 in TL in complete specimens. Mouth relatively small, subterminal; rictus restricted, does not extend beyond vertical of posterior nostril; maxillary extends to slightly beyond level of anterior orbit margin. Lips thick, papillaceous. Snout low, narrow, scarcely protruding beyond mouth; terminal and lateral angles tipped with stout tubercular scutes. Orbits large, much longer than snout, 1.2 into postorbital length; twice interorbital width. Barbel short, slender; length about 1.5 length of posterior nostril, less than suborbital width, about 3 into orbits. Suborbital region vertical, without a ridge. Underside of snout and suborbital heavily studded with large tubercular sensory papillae. Leading anterior edge of snout scaleless, but densely

covered with papillae. Pores of cephalic sensory canals fairly prominent along ventral edges of snout, suborbital, preopercle, and mandible. Preopercle broadly rounded, posterior edge inclined slightly backwards and almost forming a right angle with ventral margin. Preopercle ridge rather inconspicuous, ventral arm stout but low, joining vertical arm at a slightly acute or almost right angle. Posterior edge of interopercle exposed as a prominent scaled tab closely adjoined to ventral edge of broad subopercle.

Gill membranes broadly attached to isthmus below or slightly behind level of posterior preopercle margin, without a free posterior fold. Gill filaments long, equal to suborbital; rakers tubercular, armed with slender curved spines; first and fifth slits greatly restricted by folds of skin.

Spinous second dorsal fin ray strongly serrated along sharp leading edge; tip of first dorsal broken off, but length probably about equal to postrostral length. Second dorsal rudimentary; anal well developed. Pectoral fins broad, extend to about over fourth anal ray. Pelvic fins well developed, most rays extend to anus or beyond; outer ray thick, prolonged, extends to about seventh or eighth anal ray. First dorsal and pelvic origins about on same vertical, pectoral origin slightly in advance of this. Anal origin about below posterior margin of first dorsal. Interspace between first and second dorsals about 1.5 length base of first dorsal; anteriormost 4 or so rays of second dorsal mere stubs.

Scales strongly adherent, spinulose, uniformly covering almost all of head and body. Naked areas limited to: small areas on lower snout surface and leading upper edge; a narrow margin below front portion of suborbital; most of mandibular rami (few scattered scales posteriorly); all of branchiostegal and gular membranes. Base of first dorsal heavily covered with small scales that rise part way up fin. Scales heavily covered with relatively long, conical, moderately reclined, closely spaced spinules arranged in parallel to somewhat convergent rows; 1 or more spinules along posterior margin longer than remainder.

Teeth all small, slender, deeply embedded in papillose gum matrix, those in upper jaw in broad bands, about 7–8 rows wide, none enlarged; those in lower jaw in narrow bands 3–4 teeth wide. Upper jaw band short, not extending beyond rictus; those in lower jaw somewhat longer, extending slightly beyond rictus. Lips and oral valves strongly papillose.

Color in alcohol tawny to light brown ground; ventral surface of head pale; fin membranes dark brown. Lining of gill chamber dark brown; gills pallid. Peritoneal lining dark brown. Oral cavity pale.

Holotype a male, its testes large and well developed. Pyloric caeca slender, fairly long (to about 10 mm), 7 counted, but possibly more (stomach everted into gullet, other caeca may have been hidden from view). Coiling of alimentary canal could not be determined because of disturbed condition of internal organs. Swim bladder features not observed to avoid further damage to specimen.

DISTRIBUTION (Fig. 20).—Known only from the Galapagos in 457 m.

ETYMOLOGY.—The species is named after the collector, the late George S. Myers, distinguished ichthyologist and former professor at Stanford University.

REMARKS.—*Coryphaenoides myersi* is readily distinguished from its close relatives *C. boops* and *C. capito* by the elongated outer pelvic ray; high pelvic ray count; short abdomen; low, nonprotruding snout; small mouth; rictus not extending to below orbits; squamation; and short broad premaxillary teeth band. The general configuration of the snout and head also differs, although there is a distinct resemblance. All three species have a short low snout and similar naked areas ventrally on the head. Squamation pattern (spinulation, extent of naked area, etc.) probably more closely resembles that of *C. boops,* although there are subtle differences. *Coryphaenoides capito* has much more deciduous scales, its spinules are more erect and needlelike and in more discrete parallel to subparallel rows. *Coryphaenoides carminifer* also shows similarity in general shape, but its higher snout and greatly thickened barbel are distinguishing.

Coryphaenoides paradoxus (Smith and Radcliffe, 1912)

(Figures 3c, 24, 28)

Macrourus paradoxus Smith and Radcliffe *in* Radcliffe 1912: 115–116, pl. 25, fig. 1 (type locality off eastern Palawan, Philippines, 2,021 m).

Coryphaenoides (*Nematonurus*) *paradoxus:* Gilbert and Hubbs 1916:143 (list), 1920:409 (compiled).

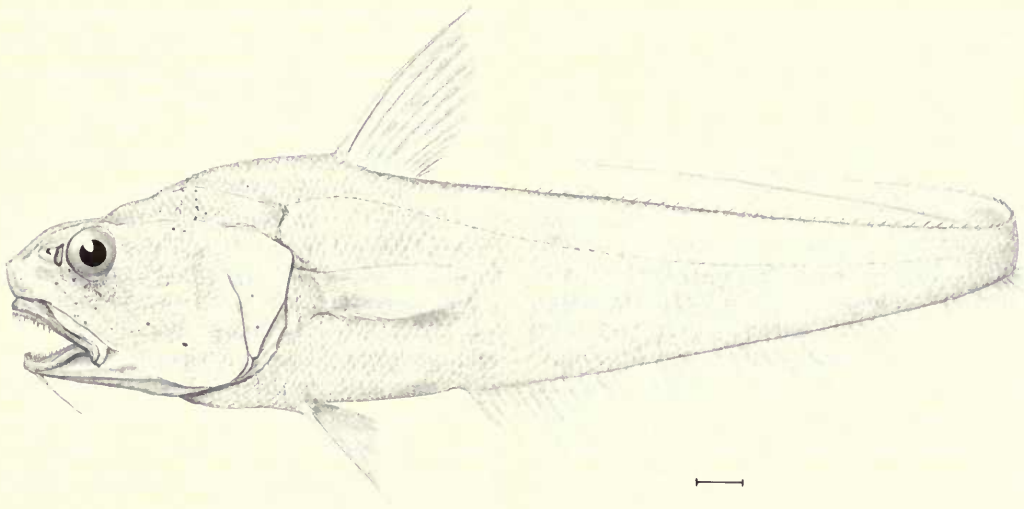


FIGURE 28. *Coryphaenoides paradoxus.* MMSU P-16528 (155 mm HL) from Nazca Ridge in 980 m. Scale bar equals 25 mm.

?*Nematonurus macrocephalus* Maul, 1951:17 (type locality Madeira).

?*Coryphaenoides macrocephalus:* Marshall and Iwamoto *in* Marshall 1973:575–578 (14 spec., Gulf of Mexico, Caribbean Sea, Guyana; 1,006–2,734 m); Merrett and Marshall 1981:241 (215 mm HL spec. from off NW Africa; 2,344–2,406 m); Anderson et al. 1985:797 (table 2) (listed from Caribbean; 3,459–3,508 m).

Coryphaenoides sp.: Parin et al. 1980:11 (765 mm TL spec. from Nazca Ridge, ICHTHYANDR sta. 1 [reported below]).

Coryphaenoides paradoxus: Wilson et al. 1985:1246 (1 spec., SIO 68-479, Darwin Guyot; about 1,600 m).

MATERIAL EXAMINED.—Holotype: USNM 72932 (116 mm HL, 585+ mm TL); Philippines, 9°13′00″N. 118°51′15″E, 1,105 fm (2,021 m); ALBATROSS sta. 5428; 3 Apr. 1909.—MMSU P-16528 (1: 155 HL, 765 TL); off Nazca Ridge, 19°40′S, 80°18′W; 980 m; R/V ICHTHYANDR sta. 1.—MMSU P-16527 (1: 166 HL, 820 TL); off Sala-y-Gomez Ridge, 25°34.4′S, 85°20.7′W; 1,070–1,100 m; R/V PROFESSOR MESIATZEV trawl 10.—SIO 68-479 (1: 268 HL, 1,200 TL); central Pacific, Darwin Seamount, 22°07.7′N, 171°36.0′E; free-vehicle setline; 16 Sep. 1968.

DIAGNOSIS.—A large species (120+ cm) of *Coryphaenoides,* subgenus *Coryphaenoides,* with 1D. II,9–11, 1P. i16–i21, V. 9–11 (rarely 8). Mouth large, almost terminal, upper jaw extends to below posterior orbit margin. Teeth prominent, an outer enlarged series on premaxillary behind which a narrow villiform band; mandibular teeth in about 3 irregular series near symphysis, becoming uniserial posteriorly. Snout low, scarcely protruding; head fully scaled except lips, gill membranes, interopercle. Orbits relatively small, about 1.5 into snout, 1.8–1.9 into interorbital space, 5.0–6.0 into HL. Interopercle barely exposed as broad fleshy tab without scales. Suborbital region vertical; no strong sharp ridges on head.

COUNTS AND MEASUREMENTS (MMSU P-16528, MMSU P-16527, SIO 68-479).—D. II, 10 + 74+, II,9 + ?, II,10 + ?; 1P. i21/i20, i21/i20, i20/i20; V. 10/10, 10/8, 10/10; GR-1 3 / 1 + 1 + 8, 3 / 1 + 1 + 8, 4 / 1 + 9; on second arch 1 + 7 / 1 + 1 + 7, ?/ 1 + 1 + 7, 2 + 8 / 1 + 8; scales 1D. 7, 8, ca. 10; 2D. 5.5, 6, 5.5; mid-1D. 5.5, 6.5, 6.5; lat.l. 36, ?, 47.

Total length 765, 820, 1,200 mm; HL 155, 166, 268 mm. Measurements in mm followed by percentage of HL in parentheses: postrostral 122, 123, 204 (74.1–77.2); snout 40.3, 46.8, 71.0 (25.5–28.2); preoral 18.4, 19.9, 27.0 (10.1–12.0); internasal 35.3, —, 46.0 (17.2–19.3); interorbital 50.1, 58.1, 71.0 (26.5–35.0); orbit 26.9, 32.5, 45.0 (16.8–19.6); suborbital 21.8, 24.1, 37 (13.8–14.5); postorbital 92.5, 95.1, 158 (57.3–59.0); orbit–preop. 89.8, 91.1, 138 (51.5–56.8); upper jaw 64.7, 71.0, 109 (40.7–42.8); barbel 26.0, 33.0, 39.0 (14.6–19.9); gill slit 10.1, 11.5, 23.0 (6.4–8.6); pre-D. 188, 193, 310 (116–119); pre-A. 248, 259, 450 (156–168); pre-V. 170, 186, 340 (108–127); V.–A. 85, 80.0, 148 (48.2–55.2); isth.–A. 158, —, 350 (100–131); body depth 133, 150, 231 (84–90); depth over A. origin 112, —, 204

(71–76); 1D.–2D. 48, 64.1, 62 (23.1–38.6); 1D. 88, 111, 148 (55.2–66.8); 1P. 78, 105, 130 (48.5–63.3); V. 100, 100, 139 (51.9–65.7).

DESCRIPTION (based primarily on 765 mm southeastern Pacific specimen, MMSU P-16528).—Head broad, greatest width about 1.7 into length; HL about 5.0 into TL. Orbits oval, longest axis vertical, horizontal diameter 5.9 into HL. Interorbital space broad, flattened in cross section. Snout low, blunt, with inconspicuous scutes at terminal and lateral angles. Mouth large, unrestricted laterally; upper jaw extends to below hind margin of orbits. Barbel well developed, slightly shorter than horizontal orbit diameter; base stout, narrows abruptly to a slender filament. Suborbital region vertical, gently rounded, without a sharp longitudinal ridge; scales covering upper half of region somewhat stouter and larger than those on lower half. Preopercle large; posterior margin slightly tilted forward from vertical; joining ventral margin in smooth curve. Preopercle ridge low, forming a slight backward extension at angle. Opercle and subopercle closely joined, forming a narrow "V." Interopercle almost entirely covered by preopercle; posterior end narrowly exposed as a broad naked, fleshy tab.

Gill membranes thick, fleshy, closely attached to isthmus without a free posterior fold. Membranes of each side join at point below posterior angle of lower jaw. First and fourth gill arches closely attached to sides of gill chamber; first and fifth gill slits consequently greatly restricted; length first (outermost) slit less than suborbital width. Gill rakers tubercular, rounded, weakly spined. Portion of shoulder girdle under gill cover heavily scaled with small spinuleless scales.

Head and body almost completely and uniformly scaled except for gill membranes and interopercle. Fins naked except at very base. Body scales large, fairly adherent, densely covered with small, short, fine, needlelike spinules in somewhat quincunx pattern or in widely divergent rows (Fig. 3c). Spinules absent along posterior margin in large specimens, most of those in large specimens with highly recurved tips. Head scales adherent and more variable in size and spinulation; some scales along head ridges somewhat larger than those surrounding, and rather coarsely spinulated and strongly adherent.

Premaxillary dentition a narrow inner band of small teeth about 3 rows wide and an outer 1 or 2 series of enlarged conical, recurved canines. Mandibular teeth clustered anteriorly, becoming 1 or 2 irregular rows posteriorly; both large and small canines at symphysis. All teeth prominent and exposed, not embedded in a thick layer of gum papillae (as in *C. bulbiceps*), extending in both jaws to posterior end of rictus.

Fins well developed. Pectoral and pelvic fin origins about on same vertical, first dorsal origin slightly behind; anal origin below that of second dorsal. Interspace between first and second dorsals about 30% HL. Second dorsal poorly developed except at tip of tail. Height of first dorsal more than half head length but less than postrostral length of head; when laid back, longest rays extend to second dorsal origin. Outer pelvic ray prolonged into filamentous tip that extends slightly beyond anal origin.

Coloration in alcohol overall dark brown with scale pockets prominently outlined in brownish black. Fins blackish to dark brown. Lips and barbel black. Gill chamber lining black; oral cavity lining blackish to dirty gray; peritoneum brownish black; gular and branchiostegal membranes dark dirty gray to blackish.

DISTRIBUTION (Fig. 24).—Philippines, mid-Pacific north of Hawaii, and Nazca Ridge in the Pacific (980–2,021 m); if *C. macrocephalus* is a synonym of *C. paradoxus*: Madeira, off NW coast of Africa, Gulf of Mexico, and Caribbean Sea in the Atlantic (1,006–3,508 m).

REMARKS AND COMPARISONS.—The surprising find of *Coryphaenoides paradoxus* in the southeastern Pacific reveals an even wider distribution than previously known. Marshall and Iwamoto (1973:578) listed several slight meristic differences between *C. paradoxus* and *C. macrocephalus* from the Gulf of Mexico and Caribbean Sea. Our comparisons of photographs of *C. macrocephalus* from the North Atlantic (Museu Municipal do Funchal no. 898 [holotype]; MCZ uncat.; UMML uncat.) with the MMSU specimens showed no definable difference. Meristic and morphometric features similarly showed no substantive differences, and in fact, the MMSU specimens agree closer in those features with the Atlantic material than with the holotype of *C. paradoxus* (USNM 72932), taken off the Philippines in 2,021 m. If the two are synonyms, then *C. paradoxus* (as *C. macrocephalus*) is known from 19 specimens from the Atlantic (see Marshall and Iwamoto 1973:575–578; Merrett and

Marshall 1981:241; Anderson et al. 1985:797). In the Pacific, only the holotype and the three specimens herein reported are known.

As with other *Coryphaenoides* species, the relationships of *C. paradoxus* are poorly known. *Coryphaenoides rudis* Günther, 1878 (reported from north of the Kermadec Islands and off New Zealand) seems very similar, as does *C. bulbiceps* from the eastern Pacific and *C. longicirrhus* (Gilbert, 1905) from Hawaii. All have similar dentition; a relatively blunt, unproduced snout; a large, almost terminal mouth; an almost flat, vertical suborbital region; an interopercle that protrudes from behind preopercle as a small fleshy naked tab; and finely spinulated scales.

Coryphaenoides paradoxus is readily distinguished from its eastern Pacific counterpart, *C. bulbiceps,* in having stronger, larger outer premaxillary teeth; smaller orbit; larger barbel; lower snout (preoral length more than 2 into interorbital space versus less than 2); and V. 9–11 versus 8.

Subgenus **Nematonurus** Günther, 1887

Nematonurus Günther, 1887:124 (as subgenus of *Macrurus*) (type species *Macrurus armatus* Hector, 1875, by subsequent designation of Jordan 1920).

DIAGNOSIS.—A subgenus of *Coryphaenoides* with usually 6 (sometimes 5 or 7) retia mirabilia. Origin of 2D. behind vertical through anus. No drumming muscles on swim bladder. Premaxillary teeth with a distinct outer row and 0–3 much smaller inner rows; mandibular teeth uniserial. Flesh relatively firm; bones stout. Scales deciduous to adherent, exposed fields with many parallel longitudinal rows of small spinules (sometimes reduced or obsolescent distally on exposed field in large individuals). Snout pointed, rather narrow, least width across supranarial ridges less than interorbital width; orbits small, less than 25% HL in adults, equal to or smaller than interorbital space and snout length. Mouth large, upper jaw more than 3 into HL, unrestricted at angles; premaxillary extends to below posterior ¼ of orbits or beyond. Abdomen long, isth.–A. greater than HL.

REMARKS.—The subgenus as here diagnosed restricts the group to four species: *C. armatus, C. lecointei, C. ferrieri,* and *C. yaquinae.* Its members are closest to species of subgenus *Chalinura,* especially in terms of squamation, dentition, and retia numbers, but they differ in having generally fewer premaxillary teeth rows, more pointed snout, longer trunk, and generally firmer bodies.

Albatrossia pectoralis has a similar dentition pattern but has a softer body, different body coloration (olive gray-brown fresh, whitish defoliated versus brown to swarthy to whitish), elongated comblike saggita otoliths, much reduced swim bladder with only two retia and gas glands, and different scales (rather elongated with much reduced spinulation).

Coryphaenoides longifilis Günther, 1887, placed in the genus *Bogoslovia* (as *B. clarki*) by Gilbert (*in* Jordan and Evermann 1898), and in genus or subgenus *Nematonurus* or *Chalinura* by most recent authors, shares similarities with *Nematonurus* spp. in dentition pattern, but other features including coloration, snout shape, fins, squamation on head and body, barbel, retia/gas gland numbers, etc., are quite different. The species probably deserves separate subgeneric or generic recognition.

Coryphaenoides armatus armatus (Hector, 1875)

Macrurus armatus Hector, 1875:81 (type locality 200 miles E of Cape Farewell, New Zealand, 400 fm [732 m]).
Macrurus (*Nematonurus*) *armatus:* Günther 1887:150, pl. 40, fig. A. (S Indian Ocean, South Pacific, Mid-Pacific).
Nematonurus armatus: Goode and Bean 1896:416 (list).
Coryphaenoides (*Nematonurus*) *armatus:* Gilbert and Hubbs 1916:143 (list).
Coryphaenoides armatus armatus: Wilson and Waples 1984: 227–237.

MATERIAL EXAMINED.—GALAPAGOS.—CAS 56589 (1: 122 mm HL, 670 mm TL); 1°48′S, 90°19′W; 3,225 m; ANTON BRUUN cr. 16, sta. 619A; bottom longline; 26–27 May 1966.—CAS 56590 (1: 131 HL, 690 TL); same data as previous except sta. 619B.—CAS 38332 (1: 95 HL, 520 TL); 2°12′S, 88°42′W; 3,160 m; ANTON BRUUN cr. 16, sta. 620B; bottom longline; 28 May 1966.

DIAGNOSIS.—A species of *Coryphaenoides,* subgenus *Nematonurus,* with bluntly pointed snout. Premaxillary teeth generally in 2 distinct rows, the outer series enlarged, the inner much smaller and sometimes lost in large individuals; mandibular teeth in 1 row, the tips rather blunt and flanged. Head pores well developed. Most ventral surfaces of head naked. Scales rather deciduous, spinules small, low, absent from posterior margin of exposed field, often reduced to

low horizontal ridges in adults. 1D. II,8–9; 1P. i17–i21 (usually i20); orbit 18–27% HL; interorbital 22.0–29.9; 1D.–2D. 45.1–95.1

Counts and Measurements (from 3 SE Pacific specimens only, CAS 38332 first, CAS 56589 second, CAS 56590 third).—D. II,8 + 105, II,9 + 96, II,8 + 94; 1P. i19/i20, i20/i20, i18/i20; V. 10/10, 10/10, 7/10 (left fin probably abnormal); A. 105, 110, 104; GR-1 7 / 2 + 1 + 9, ca. 10 / 2 + 1 + 10, 6 / 2 + 9, GR-2 2 + 11 / 2 + 10, 1 + 10 / 1 + 1 + 9, 1 + 1 + 7 / 2 + 1 + 8; scales 1D. 9, 9, 9.5; 2D. 10, 9, 9; mid-1D. 7.5, 7.5, 6.5; lat.l. 34, 30, 30.

Total length 520, 670, 690 mm; HL 95, 122, 131 mm. The following in percent of HL: postrostral 77.9, 80.4, 80.2; snout 26.4, 21.8, 22.9; preoral 13.4, 12.8, 11.5; internasal 17.5, 16.4, 16.0; interorbital 26.9, 24.4, 25.2; orbit 21.6, 20.5, 19.8; suborbital 11.0, 10.6, 8.9; postorbital 56.4, 58.9, 56.5; orbit–preop. 45.9, 49.9, 49.2; upper jaw 39.0, 38.3, 38.4; barbel 14.9, 15.9, 9.0; gill slit 16.3, 15.7, 15.8; pre-D. 124, 131, 130; pre-A. 196, 198, 196; pre-V. 120, 115, 111; V.–A. 81, 90, 90; isth.–A. 129, 151, 151; body depth 93, 93, 96; 1D.–2D. 54, 83, 81; 1D. 68, 77, 67; 1P. 50, 66, 63; V. 65, 66, 69.

Remarks.—This species has been adequately described and illustrated by several authors, including Iwamoto and Stein (1974), Marshall (1973), Nybelin (1957), and Parr (1946). Extensive synonymies are provided by Parr (1946), Grey (1956), and Marshall (1973). Wilson and Waples (1983) recently described characters to better distinguish the species from *C. yaquinae* Iwamoto and Stein, 1974, and designated a lectotype for *C. variabilis* Günther, 1878, from a type series that included both *C. yaquinae* and *C. armatus,* as well as *C. leptolepis* Günther, 1878.

Wilson and Waples (1984) subsequently recognized two subspecies of *C. armatus*: *C. a. variabilis* (Günther, 1878) from the North Pacific and *C. a. armatus* (Hector, 1875) from all other areas. In the eastern Pacific, the Gulf of Panama separates the two subspecies. The two authors found the North Pacific subspecies to have a narrower interorbital space, shorter dorsal interspace, more 1D. rays (II,9–10 versus II,8–9) and more 1P. rays (21–23 total of both sides, versus 18–21) than in *C. a. armatus.* In addition to these differences, our *C. a. armatus* from the southeastern Pacific are paler in overall color (light brown to tawny in alcohol compared with dark brown to almost swarthy in *C. a. variabilis*) as well as in fin color (blackish in *C. a. variabilis* cf. pale with blackish edges on serrated dorsal spine, uppermost pectoral ray, outer pelvic ray, and distal edges of anal fin in *C. a. armatus*), and the serrations on the 1D. spine are much better developed in our three southeastern Pacific specimens than in our *C. a. variabilis* specimens from the northeastern Pacific.

For references to much of the recent published information on biochemical, physiological, morphological, ecological, and life history aspects of this, the best known, most extensively studied abyssal macrourid, see Wilson and Waples (1983, 1984), and Wilson and Smith (1984).

Subgenus **Chalinura** Goode and Bean, 1883

Chalinura Goode and Bean, 1883:24 (type species *Chalinura simula* Goode and Bean, 1883, by original designation).

Goode and Bean (1883) provided a good diagnosis for their new genus *Chalinura,* which Parr (1946) expanded based on his experience with western Atlantic species. Parr, however, included *C. carapinus,* which Nybelin (1957) subsequently relegated to the genus *Lionurus,* and failed to consider in his diagnosis characters of other *Chalinura.* We believe the following combination of characters distinguishes the eight or so members of this subgenus from other *Coryphaenoides.*

Diagnosis.—A subgenus of *Coryphaenoides* with 5–6 retia mirabilia. Origin of A. below or forward of 1D.–2D. interspace. No drumming muscles on swim bladder. Premaxillary teeth in moderately wide band of small teeth with an outer row of enlarged spaced canines; mandibular teeth moderate in size, in 1 row (sometimes irregular double row). Flesh and bones rather soft. Scales deciduous; small sharp conical spinules arranged in parallel longitudinal rows, spinules sometimes greatly reduced. Snout usually bluntly pointed or somewhat rounded, width between supranarial ridges usually less than interorbital width; orbits small, about 25% HL or less, less than interorbital. Mouth large, upper jaw usually more than 40% HL; mouth opening not restricted; upper jaw extends to or beyond vertical through posterior ¼ of orbit. Abdomen moderate to short, isth.–A. usually less than HL. Gill membranes narrowly connected to isthmus

with a broad posterior free fold. Outer gill slit moderately restricted, 14–30% HL. Gill rakers usually 12–17 on inner series of first arch.

Coryphaenoides fernandezianus (Günther, 1878)
(Figure 11)

Macrurus (Chalinurus) fernandezianus Günther, 1887:145, pl. 38, fig. B (type locality S of Juan Fernandez Is.; CHALLENGER sta. 300; 1,375 fm [2,515 m]).
Chalinura fernandezianus: Goode and Bean 1896:412.
Coryphaenoides fernandezianus: Gilbert and Hubbs 1920:143.

REMARKS.—We examined no representative of this species and none has been recorded since the capture of the holotype off Juan Fernandez Island. Its relationship to other members of the subgenus *Chalinura* must be examined. The notably high snout resembles that of *C. brevibarbis* Goode and Bean, 1883, but its barbel is much longer than in that species and its head is not as broad. *Coryphaenoides fernandezianus* appears to differ from *C. leptolepis* (Günther, 1877) in its higher snout, shorter barbel, and less humpbacked dorsal profile, and from *C. murrayi* Günther, 1878, in its fewer pelvic rays (10 versus 11–12 in *C. murrayi*). (See also comparison with *C. oreinos*.)

Subgenus **Lionurus** Günther, 1887

Lionurus Günther, 1887:124 (as subgenus of *Macrurus*) (type species *Coryphaenoides filicauda* Günther, 1878, by subsequent designation of Goode and Bean 1896).

DIAGNOSIS.—A subgenus of *Coryphaenoides* with 6 retia mirabilia. Origin of 2D. behind vertical through anus. No drumming muscles on swim bladder. Premaxillary teeth small, in narrow band, outer teeth somewhat larger than those more medial; mandibular teeth in narrow band (about 4 rows wide at symphysis) that tapers rapidly to a single row laterally. Flesh rather soft; bones of head weak and thin. Scales highly deciduous, exposed fields with few (1–5) low ridges sometimes armed with a few greatly reclined spinules; 1 or 2 adjacent parallel ridges on either side of medial row; many scales completely smooth. Snout pointed, broad across supranarial ridges, width about equal to interorbital width; orbits small, less than 25% HL in adults, much less than broad interorbital space. Mouth moderate sized, unrestricted at posterior angles; upper jaw about 3 into HL, extends to below posterior ¼ of orbits or beyond. Abdomen moderate in length, distance isth.–A. about equal to or less than HL.

REMARKS.—This subgenus includes only two known species: *C. filicauda* and *C. carapinus* (but see Remarks in description of the former species). Its relationships are probably closest to subgenus *Chalinura*. Members of the two subgenera share: relatively soft flesh; small eyes; unrestricted, relatively large mouth; extensive naked areas on underside of head; generally weak scale spinulation; six retia mirabilia; and similar premaxillary dentition.

Lionurus species are among the deepest-living grenadiers; the soft flesh, weak bones, small eyes, pale coloration, and reduced spinulation on scales are probably responses to living conditions at abyssal depths.

Larval and juvenile stages of *Lionurus carapinus* and *Lionurus* (?) sp. from the eastern North Atlantic were described by Merrett (1978).

Coryphaenoides filicauda Günther, 1878
(Figures 15, 29)

Coryphaenoides filicauda Günther, 1878:27 (type locality: "both sides of the South American continent; Antarctic Ocean. [Stations 157, 299, 325.] 1,800–2,650 fathoms.").
Macrurus (Lionurus) filicauda: Günther 1887:141, pl. 34, fig. B. (CHALLENGER sta. 146, 157, 299, 323, 325; 2,515–4,846 m).
Lionurus filicauda: Goode and Bean 1896:409, fig. 342 (compiled).
Lionurus (?) [sic.]: Parin and Makushok 1973:80 (one spec., 215 mm TL, sta. 239A, "Proba" 137, presumed lost, but subsequently found by Y. N. Shcherbachev; see Material Examined below).

MATERIAL EXAMINED.—Lectotype: BMNH 1887. 12.7:96 (65.3 mm HL, 372 mm TL); off Valparaiso, Chile, 33°32′S, 74°43′W; 3,951 m; CHALLENGER sta. 299. Paralectotype: BMNH 1887.12.7:95 (49.1 HL, 287 TL); S Atlantic off Rio de La Plata, 36°44′S, 46°16′W; 4,846 m; 2 Mar. 1876.

Other material.—CHILE.—MMSU P-16540 (1: 40.3 mm HL, 215 mm TL); 23°51′S, 71°01′W; 4,550 m; AKADEMIK KURCHATOV sta. 239a ("Proba" 137).—LACM 10189-1 (1: 25 HL, 145 TL); off Chiloe I., 42°57′S, 75°33′W; 3,651 m; ELTANIN sta. 334; 27 Nov. 1962. NEW ZEALAND.—LACM 11333-2 (1: 62.5 HL, 265+ TL); SW of South Is., 46°40′S, 165°18′E; 2,470 m; ELTANIN sta. 1844; 15 Feb. 1966. ANTARCTIC.—LACM 11436-2 (1: 70.5 HL, 405+ TL); SW Pacific sector, 57°55′S, 153°58′E; 3,422 m; ELTANIN sta. 1969; 13 Feb. 1967.—LACM 10862-1 (1: 43.4 HL, 270 TL); SW Pacific sector, 51°50′S, 159°50′W; 4,667 m; ELTANIN sta. 1184; 3–4 Aug. 1964.—LACM 11761-1 (1: 62.2 HL, 295 TL); SE Pacific sector, 50°51′S, 104°53′W; 3,923 m; ELTANIN cr. 20, sta. 26; 25 Oct. 1965.—LACM 10747-3 (2: 73.0–73.0 HL,

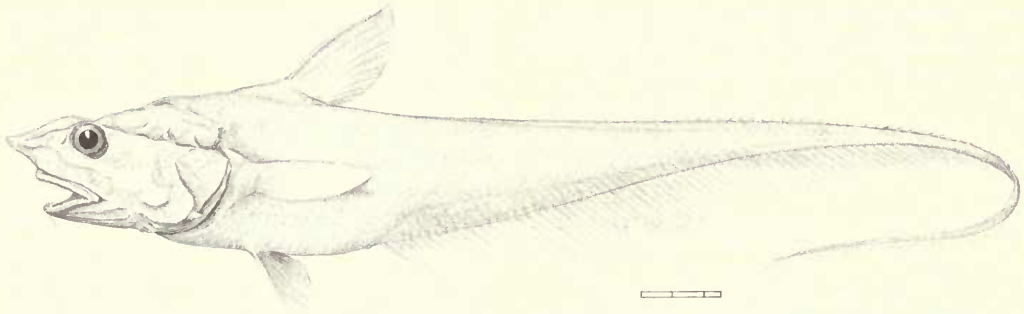


FIGURE 29. *Coryphaenoides filicauda.* Composite drawing of LACM 11436-2 (70.5 mm HL, 405+ mm TL) and LACM 10747-3 (73.0 mm HL, 355 mm TL) from Antarctic waters. Scale bar equals 25 mm.

299–355 TL); SW Atlantic sector, 58°54′S, 53°51′W; 3,931 m; ELTANIN sta. 1509; 25–26 Jan. 1966.—LACM 10749-1 (1: 70.0 HL, 378 TL); SW Atlantic sector, 59°01′S, 52°00′W; 3,510 m; ELTANIN sta. 1511; 26 Jan. 1966. AUSTRALIA.—MMSU P-16539 (1: 41 HL, 230 TL); off SW coast Tasmania, 43°37′S, 144°04′E; 4,464 m; DMITRY MENDELEEV sta. 1349.—MMSU P-16538 (1: 27 HL, 120 TL); Great Australian Bight, 35°21′S, 128°42′E; 5,070 m; DMITRY MENDELEEV sta. 1358.

DIAGNOSIS.—A species of subgenus *Lionurus* with GR-1 3–6 total outer / 8–10 total inner; outer gill rakers reduced to minute prickles; orbits 15.6–18.7% HL; barbel 4.1–11.9% HL; leading edge of spinous 1D. ray smooth except for a few low denticles distally. Overall coloration pale whitish gray.

COUNTS AND MEASUREMENTS (13 specimens).—1D. II,8–10; 1P. i16–i19; V. 9–10. GR-1 (3–6) / (1–2) + 1 + (7–9) [8–10 total], GR-2 (1–2) + 1 + (7–8) [8–9 total] / (1–2) + 1 + (7–8) [9–10 total]. Total length 120–405+ mm; HL 25.0–73.0 mm. The following in percent HL: postrostral 66.6–69.2; snout 32.6–38.0; preoral 16.1–23.0; internasal 21.1–28.1; interorbital 30.7–33.1; orbit 15.6–20.0; suborbital 11.6–16.6; postorbital 46.7–53.6; orbit–preop. 45.7–50.0; upper jaw 32.5–36.8; barbel 3.8–8.8; gill slit 10.0–17.5; pre-D. 113–127; pre-V. 108–133; pre-A. 140–177; V.–A. 33–53; isth.–A. 76–106; body depth 62–87 (100); 1D.–2D. 53.8–83.4; 1D. 56–70; 1P. 51–69; V. 43–60; nostril 4.6–6.0.

DESCRIPTION.—Head somewhat depressed, broad, bones rather soft; width across opercles about equal to depth at beginning of nape. Body notably soft fleshed, long and slender. Trunk rather long, distance isth.–A. about equal to HL in larger specimens (+60 mm HL). Head about 6 in TL, greatest depth about 7 in TL in larger specimens. Snout pointed, protruding well beyond jaws a distance more than ⅔ length of orbits. Orbits small, about 2 into broad interorbital space in larger specimens; shape oval, longest axis horizontal. Jaws long, extending to below hind ¼ of orbit; rictus to below or beyond midorbit. Barbel minute, length about equal to diameter of posterior nostril. Preopercle large, posterior margin inclined, free posteroventral margin crenulated. Interopercle exposed posteriorly as thin, slender pointed flap adjoined to subopercle.

Gill membranes narrowly attached to isthmus; opercular opening wide, little restricted, extends forward to below posterior end of lower jaw. Outer gill slit fairly wide, slightly smaller than orbit diameter. Gill rakers of outer series few rudimentary prickles on low ridges; inner series tubercular, spiny. Gill filaments short, slightly longer than ½ orbit diameter.

Scales large, thin; the few remaining on some specimens have either a single median ridge of 1–3 greatly reclined spinules or surface entirely smooth. About 7 transverse rows across interorbital space; 5–6.5 rows below midbase 1D., about 26–33 over distance equal to predorsal length. No stout scutelike scales on head ridges; leading edge of snout with a few small, deeply embedded spiny scales. Underside of snout mostly naked; a few large cycloid scales on suborbital and mandibular rami.

Jaw teeth small, slender, in narrow bands. Premaxillary band 4–5 teeth wide near symphysis; band gradually tapers to 2 irregular rows posteriorly; outer teeth somewhat larger than those more medial. Mandibular teeth band about 4

rows wide anteriorly tapering rapidly to a single row posterolaterally.

Fins fairly well developed. Height 1D. somewhat more than postorbital length; leading edge of second spinous ray smooth except for a few small low denticles distally. Pectoral fin and filamentous outer pelvic ray extend to level of vent. First dorsal and V. origins about on same vertical, pectoral origin well in advance of this. Interspace between dorsals wide, about equal to postrostral length; 2D. rudimentary throughout, origin over 7th–11th A. ray. Flesh over anal pterygiophores jellylike, translucent.

Coloration in alcohol whitish gray overall. Fins pale except for uppermost 1P. ray, tip of spinous second 1D. ray, and outer V. ray, which are blackish. Branchiostegal membranes, barbel, and rim of vent brownish gray to dark brown. Branchial and peritoneal linings black; oral lining and gill arches dark gray to gray-brown.

DISTRIBUTION (Fig. 15).—High latitudes of southern hemisphere; known from Atlantic, Indian, and Pacific oceans. Collected in abyssal waters off Chile, Argentina, South Shetland Islands, New Zealand, and southern Australia. Depth range 2,470–5,070 m; primary range around 3,500–5,000 m.

REMARKS AND COMPARISONS.—This abyssal species has a broad distribution in the Southern Ocean and was previously recorded from the southern part of the Pacific coast of Chile from CHALLENGER sta. 299 (lectotype). Two additional specimens from Chile are herein recorded.

Material from outside the southeastern Pacific examined at MMSU and LACM revealed the presence of another species of the subgenus *Lionurus* in the southern hemisphere. These specimens were indistinguishable from *C.* (*L.*) *carapinus* (Goode and Bean, 1883). These southern hemisphere "*C. carapinus*" were captured at somewhat shallower depths (1,700–3,064 m) than our *C. filicauda* specimens.

Among these additional specimens was a 259-mm specimen (ZIL 11720, formerly deposited in the Zoological Institute in Leningrad) labeled as "*C. filicauda*" and trawled at CHALLENGER sta. 146 in the southwestern Atlantic. The station (in 2,515 m) is one of those listed by Günther (1887:141) at which representatives of *C. filicauda* were procured. This particular specimen, however, is indistinguishable from *C. carapinus*.

The type specimen of *C. filicauda* from Chile (CHALLENGER sta. 299), taken at a depth of 3,951 m, was designated as the lectotype by Grey (1956:184). Our concept of *C. filicauda* conforms to that specimen, which was examined (by TI) through the courtesy of A. Wheeler (BMNH). Nybelin's (1957) specimens of *Lionurus carapinus euabyssalis,* trawled from depths between 4,255 and 5,610 m in the northeastern Atlantic, are problematic. Their vertical distribution (much deeper than in *C. carapinus*) suggests *C. filicauda,* but Nybelin's specimens are in such poor condition that we cannot determine their identity based on his description.

As we see it, *Coryphaenoides filicauda* is distinguished from *C. carapinus* by its having fewer outer gill rakers on the first arch (3–6 versus 6–11), these being rudimentary prickles compared with the tablike rakers in *C. carapinus*; a softer, more translucent body; fewer spinations on the spinous dorsal ray; a shorter outer gill slit (11.9–14.6% HL versus 14.6–18.5%); and a narrower interorbital (29.3–32.2% HL versus 30.8–40.1%).

LITERATURE CITED

ALCOCK, A. 1889. Natural history notes from H.M. Indian Marine Survey Steamer 'Investigator,' Commander Alfred Carpenter, R.N., D.S.O., commanding. No. 13. On the bathybial fishes of the Bay of Bengal and neighboring waters, obtained during the seasons 1885–1889. Ann. Mag. Nat. Hist., ser. 6, 6(23):376–399.

———. 1890a. Natural history notes from H.M. Indian Marine Survey Steamer 'Investigator,' Commander C. F. Hoskyn, R. N., commanding. No. 18. On the bathybial fishes of the Arabian Sea, obtained during the season 1889–1890. Ann. Mag. Nat. Hist., ser. 6, 6(34):295–311.

———. 1890b. On the deep-sea fishes collected by the "Investigator" in 1890–91. Ann. Mag. Nat. Hist., ser. 6, 8:16–34; 119–138, pls. vii–viii.

ANDERSON, M. E., R. E. CRABTREE, H. J. CARTER, K. J. SULAK, AND M. D. RICHARDSON. 1985. Distribution of demersal fishes of the Caribbean Sea found below 2,000 meters. Bull. Mar. Sci. 37(3):794–807.

BARNARD, K. H. 1925. A monograph of the marine fishes of South Africa. Pt. 1 (Amphioxus, Cyclostomata, Elasmobranchii, and Teleostei—Isospondyli to Heterostomata). Ann. S. Afr. Mus. 21(pt. 1):1–418.

BEAN, T. H. 1884. Notes on some fishes collected in Washington Territory, including a new species of *Macrurus.* Proc. U.S. Natl. Mus. 6(1883):362–364.

CHIRICHIGNO, N. 1968. Nuevos registros para la ictiofauna marina del Perú. Bol. Inst. Mar. Perú (Callao) 1(8):377–504.

———. 1969. Lista sistemática de los peces marinos comunes para Ecuador-Perú-Chile. Conferencia Sobre Explotación y Conservación de las Riquezas Marítimas del Pacífico Sur. G. Morsom, S.A., Lima. 108 pp.

———. 1974. Clave para identificar los peces marinos del Peru. Inf. Inst. Mar Perú (Callao) 44:1–387.

Chirichigno, N. and T. Iwamoto. 1977. *Coryphaenoides delsolari,* a new species of macrourid fish from the Pacific coast of South America. Proc. Biol. Soc. Wash. 89(45):519–528, figs. 1–3.

Cohen, D. M. and R. L. Haedrich. 1983. The fish fauna of the Galapagos thermal vent region. Deep-Sea Res. 30(4A): 371–379.

Dollo, L. 1900. *Macrurus lecointei,* poisson abyssal nouveau recueilli par cette expédition. Expédition Antarctique Belge. Bull. Acad. R. Belg. (Sci.) (6):1–20.

———. 1909. *Cynomacrurus piriei,* poisson abyssal nouveau recueilli par l'Expédition Antarctique Nationale Ecossaise. Proc. R. Soc. Edinb. 29(4):316–326.

Dooley, J. K. 1979. A rare and unusually large macrourid fish from the Canary Islands. Copeia 1979(3):541–542.

Fahay, M. P. and D. F. Markle. 1985. Gadiformes: development and relationships. Pp. 265–283 *in* Ontogeny and development of fishes. Spec. Publ. Am. Soc. Ich. Herp. 1. 760 pp.

Fraser-Brunner, A. 1935. New or rare fishes from the Irish Atlantic Slope. Proc. R. Ir. Acad. Sect. B, 42(8):319–326.

Garman, S. H. 1899. Report on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross" during 1891. Lieut.-Commander Z. L Tanner, U.S.N., commanding. Part 26, The fishes. Mem. Mus. Comp. Zool. Harv. 26:1–431, pls. 1–84, A–N.

Giglioli, E. H. 1893. Di una nuova specie di Macrurid appartenente alla fauna abissale del Mediterraneo. Zool. Anz. 16(428):343–345.

Gilbert, C. H. 1890. A preliminary report on the fishes collected by the steamer "Albatross" on the Pacific coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species. Proc. U.S. Natl. Mus. 13:49–126.

———. 1892. Scientific results of explorations by the U.S. Fish Commission Steamer "Albatross." No. 22. Descriptions of thirty-four new species of fishes collected in 1888 and 1889, principally among the Santa Barbara Islands and in the Gulf of California. Proc. U.S. Natl. Mus. 14:539–566.

———. 1895. The ichthyological collections of the steamer "Albatross" during the years 1890 and 1891. Rep. U.S. Comm. Fish. 1893, 19:393–476, pls. 20–35.

———. 1905. The deep-sea fishes of the Hawaiian Islands. Pp. 575–713, figs. 230–276, pls. 66–101 *in* The aquatic resources of the Hawaiian islands. D. S. Jordan and B. W. Evermann, eds. Bull. U.S. Fish Comm. 1903, 22(pt. 2, sect. 2).

Gilbert, C. H. and C. L. Hubbs. 1916. Report on the Japanese macrouroid fishes collected by the United States fisheries steamer "Albatross" in 1906, with a synopsis of the genera. Proc. U.S. Natl. Mus. 51:135–214, pls. 8–11.

———. 1920. The macrourid fishes of the Philippine Islands and the East Indies. U.S. Natl. Mus. Bull. 100, 1(pt. 7):369–588, figs. 1–40.

Gilbert, C. H. and W. F. Thompson. 1916. Family Macrouridae. Pp. 471–476, pls. 5, 6 *in* W. F. Thompson, ed., Fishes collected by the United States Bureau of Fisheries Steamer "Albatross" during 1888, between Montevideo, Uruguay, and Tome, Chile, on the voyage through the Straits of Magellan. Proc. U.S. Natl. Mus. 50:401–476, pls. 2–6.

Goode, G. B. and T. H. Bean. 1883. Reports on the results of dredging under the supervision of Alexander Agassiz, on the east coast of the U.S. XIX—Report on the fishes. Bull. Mus. Comp. Zool. Harv. 10(5):183–226.

———. 1896. Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world . . . . Smithson. Contrib. Knowl. 1895 [1896], 30(981), 1(text):1–553; 2(atlas):1–26, pls. 1–123. [Also issued as U.S. Natl. Mus. Spec. Bull. 2, and Mem. Mus. Comp. Zool. Harv. 22.]

Grey, M. 1956. The distribution of fishes found below a depth of 2,000 meters. Fieldiana Zool. 36(2):74–336.

Gunnerus, J. E. 1765. Efterretning om berglaxen, en rar norsk fishk, som kunde kaldes: *Coryphaenoides rupestris.* K. Norske Vidensk. Selsk. Skifter Trondhjem 3(4):40–58.

Günther, A. 1877. Preliminary notes on new fishes collected in Japan during the expedition of H.M.S. "Challenger." Ann. Mag. Nat. Hist., ser. 4, 20:433–447.

———. 1878. Preliminary notices of deep-sea fishes collected during the voyage of H.M.S. "Challenger." Ann. Mag. Nat. Hist., ser. 5, 2:17–28.

———. 1887. Report on the deep-sea fishes collected by H.M.S. Challenger during the years 1873–76. Rep. Sci. Res. Challenger 22(Zool.) (pt. 1) [text]:1–335; (pt. 2) [plates]: pls. 1–73.

Hector, J. 1875. Descriptions of five new species of fishes obtained in New Zealand seas by H.M.S. "Challenger" expedition. Ann. Mag. Nat. Hist., ser. 4, 15:78–82.

Horibe, S. 1983. Technique and studies of marine environmental assessment. Results of tests of automatic floating deep-sea sampling device in deep water (6,000 m). Biological and collecting experiments. Spec. Rep. Ocean Res. Inst., Tokyo Univ., March, 23 pp., 1 table. [In Japanese.]

Hubbs, C. L. and T. Iwamoto. 1977. A new genus (*Mesobius*), and three new bathypelagic species of Macrouridae (Pisces, Gadiformes) from the Pacific Ocean. Proc. Calif. Acad. Sci., ser. 4, 41(7):233–251, figs. 1–11.

Iwamoto, T. 1970. The R/V PILLSBURY Deep-Sea Biological Expedition to the Gulf of Guinea, 1964–65. 19. Macrourid fishes of the Gulf of Guinea. Stud. Trop. Oceanogr. (Miami) 4(pt. 2):316–431, figs. 1–27.

———. 1978. Eastern Pacific macrourids of the genus *Coelorinchus* Giorna (Pisces: Gadiformes), with description of a new species from Chile. Proc. Calif. Acad. Sci., ser. 4, 4(12):307–337, figs. 1–20.

———. 1979. Eastern Pacific macrourine grenadiers with seven branchiostegal rays (Pisces: Macrouridae). Proc. Calif. Acad. Sci. 42(5):135–179, figs. 1–18.

Iwamoto, T. and D. L. Stein. 1974. A systematic review of the rattail fishes (Macrouridae: Gadiformes) from Oregon and adjacent waters. Occas. Pap. Calif. Acad. Sci. 111:1–79, figs. 1–25.

Jordan, D. S. 1920. The genera of fishes. Pt. IV. From 1881 to 1920, thirty-nine years, with the accepted type of each . . . . Stanford Univ. Publ., Univ. Ser. pp. 415–576, i–xviii.

Jordan, D. S. and B. W. Evermann. 1898. The fishes of North and Middle America. Bull. U.S. Natl. Mus. 47(3): 2183–3134.

Leviton, A. E., R. H . Gibbs, Jr., E. Heal, and C. E. Dawson. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985(3):802–832.

MacDonald, K. C. and J. D. Mudie. 1974. Microearthquakes on the Galapagos spreading centre and the seismicity

of fast-spreading ridges. Geophys. J. R. Astrophys. Soc. 36: 245–257.

MAKUSHOK, V. M. 1967. Whiptails (family Macrouridae or Coryphaenoididae Auct.). Part II, Chap. IV. Pp. 3–273 *in* Biology of the Pacific Ocean, Book III, Fishes of the open waters. V. G. Kort, chief ed. Moscow. [Transl. from Russian, U.S. Naval Oceanogr. Off. Transl. 528, Washington, D.C.]

———. 1976. The new rattail *Coryphaenoides subserrulatus* sp.n. (Macrouridae, Osteichthys) from the area south of New Zealand. Pp. 144–155 *in* Biology and distribution of tropical deep-sea fishes. N. V. Parin, ed. Tr. Inst. Okeanol. Akad. Nauk SSSR, Moscow. 104, 336 pp. [In Russian.]

MARSHALL, N. B. 1965. Systematic and biological studies of the macrourid fishes, Anacanthini-Teleostii. Deep-Sea Res. 12(3):299–322.

———. 1973. Family Macrouridae. Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res. (1) (pt. 6): 496–665.

MARSHALL, N. B. AND T. IWAMOTO. 1973. Genus *Coryphaenoides*. Pp. 565–600 *in* Family Macrouridae. Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res. (1) (pt. 6).

MAUL, G. E. 1951. Monografia dos peixes do Museu Municipal do Funchal. Família Macrouridae e Merlucciidae. Bol. Mus. Munic. Funchal (5) (art. 12):5–55, figs.

MEAD, G. W., E. BERTELSEN, AND D. M. COHEN. 1964. Reproduction among deep-sea fishes. Deep-Sea Res. 11:569–596.

MERRETT, N. 1978. On the identity and pelagic occurrence of larval and juvenile stages of rattail fishes (family Macrouridae) from 60°N, 20°W. Deep-Sea Res. 25:147–160.

———. 1983. A new species of the deep-sea fish genus *Coryphaenoides* Gunnerus (Macrouridae) from the tropical eastern North Atlantic and its relationship with *C.* (*Coryphaenoides*) *marshalli* Iwamoto, 1970. J. Fish Biol. 22:265–278.

MERRETT, N. AND N. B. MARSHALL. 1981. Observations on the ecology of deep-sea bottom-living fishes collected off northwest Africa (08°–27°N). Prog. Oceanogr. 9:185–244.

MERRETT, N., YU. I. SAZONOV, AND YU. N. SHCHERBACHEV. 1983. A new genus and species of rattail from the eastern North Atlantic and eastern Indian Ocean, with notes on its ecology. J. Fish Biol. 22:549–561.

NORMAN, J. R. 1939. Fishes. Sci. Rep. John Murray Exped. 1933–1934, 7(Zool.)(1):1–116.

NYBELIN, O. 1957. Deep-sea bottomfishes. Rep. Swed. D-S. Exped. 1947–48, 2(Zool.)(20):247–345, pls. 1–7.

OKAMURA, O. 1970*a*. Fauna Japonica. Macrourina (Pisces). Academic Press, Tokyo. 216 pp., 64 pls.

———. 1970*b*. Studies on the macrouroid fishes of Japan. Morphology, ecology and phylogeny. Rep. Usa Mar. Biol. Stn. 17(1–2):1–179.

PARIN, N. V., G. A. GOLOVAN, N. P. PAKHORUKOV, YU. I. SAZONOV, AND YU. N. SHCHERBACHEV. 1980. Fishes from the Nazca and Sala-y-Gomez underwater ridges collected in cruise of R/V "Ikhtiandr." Pp. 5–18 *in* Fishes of the open ocean. N. V. Parin, ed. Inst. Okeanol. Akad. Nauk SSSR, Moscow. 120 pp. [In Russian.]

PARIN, N. V. AND V. M. MAKUSHOK. 1973. Deep-sea bottom fishes collected during the 4th cruise of the R/V "Akademik Kurchatov" in the south-eastern part of the Pacific Ocean. Tr. Inst. Okeanol. Akad. Nauk SSSR 94:173–187. [In Russian.]

PARIN, N. V. AND YU. I. SAZONOV. 1983. Deep-sea fishes collected during a cruise of R/V "Professor Mesiatzev" along the Peruvian coast in 1972. Pp. 79–91 *in* Insufficiently studied fishes of the open ocean. Inst. Okeanol. Akad. Nauk SSSR, Moscow. [In Russian.]

PARR, A. E. 1946. The Macrouridae of the western North Atlantic and Central American seas. Bull. Bingham Oceanogr. Coll. Yale Univ. 10(art. 1):1–99.

PEQUEÑO, G. 1971. Sinopsis de Macrouriformes de Chile (Pisces, Teleostomi). Bol. Mus. Nac. Hist. Nat. Chile 32: 269–298, figs. 1–17, maps. 1–3.

RADCLIFFE, L. 1912. Descriptions of a new family, two new genera, and twenty-nine new species of anacanthine fishes from the Philippine Islands and contiguous waters. Proc. U.S. Natl. Mus. 43:105–140, pls. 22–31.

REGAN, C. T. 1913. The Antarctic fishes of the Scottish National Antarctic Expedition. Trans. R. Soc. Edinb. 49(pt. 2) (2):229–292, pls. 1–11.

RICHARDSON, J. 1846. Fishes. The zoology of the voyage of H.M.S. *Erebus* and *Terror*, 2: viii + 739 pp., 40 pls., E. W. Janson, London.

STEIN, D. L. 1980. Description and occurrence of macrourid larvae and juveniles in the northeast Pacific Ocean off Oregon, U.S.A. Deep-Sea Res. 17:889–900.

STEIN, D. L. AND W. G. PEARCY. 1982. Aspects of reproduction, early life history, and biology of macrourid fishes off Oregon, U.S.A. Deep-Sea Res. 29:1313–1329.

STEINDACHNER, F. AND L. DÖDERLEIN. 1887. Beiträge zur Kenntniss der Fische Japan's, (IV). Denkschr. Nat.-Naturwiss. Akad. Wiss. Wien 53:257–296, pls. 1–4.

VAILLANT, L. L. 1888. Expéditions scientifiques de TRAVAILLEUR et du TALISMAN pendant les années 1880, 1881, 1882, 1883. Poissons. G. Masson, Paris. 406 pp., 28 pls.

WEBER, M. 1913. Die Fische der SIBOGA-Expedition. Siboga Exped. 57:1–719, pls. 1–12.

WEBER, M. AND L. F. DE BEAUFORT. 1929. The fishes of the Indo-Australian Archipelago 5. E. J. Brill, Leiden. 458 pp.

WILSON, R. R., JR. AND K. L. SMITH. 1984. Effect of near-bottom currents on detection of bait by the abyssal grenadier fishes *Coryphaenoides* spp., recorded *in situ* with a video camera on a free vehicle. Mar. Biol. 84:83–91, figs. 1–3.

WILSON, R. R., JR., K. L. SMITH, AND R. H. ROSENBLATT. 1985. Megafauna associated with bathyal seamounts in the central North Pacific Ocean. Deep-Sea Res. 32(10):1243–1254.

WILSON, R. R., JR. AND R. S. WAPLES. 1983. Distribution, morphology, and biochemical genetics of *Coryphaenoides armatus* and *C. yaquinae* (Pisces: Macrouridae) in the central and eastern North Pacific. Deep-Sea Res. 130:1127–1145.

———. 1984. Electrophoretic and biometric variability in the abyssal grenadier *Coryphaenoides armatus* of the western North Atlantic, eastern South Pacific and eastern North Pacific oceans. Mar. Biol. 80:227–237.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 4, pp. 83-88, 9 figs., 2 tables. February 5, 1988

A NEW SPECIES AND NEW RECORDS OF SCHIZOMIDS FROM THE CENTRAL COASTAL CALIFORNIA (SCHIZOMIDA: SCHIZOMIDAE: *SCHIZOMUS*)

By

Thomas S. Briggs and Kevin Hom

Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118-9961

ABSTRACT: **A new species of schizomid, *Schizomus secoensis*, discovered in Monterey County, California, is the most northwestern member of the order Schizomida in North America. Five new records for *Schizomus belkini* (McDonald and Hogue) extend its range northward to the vicinity of San Luis Obispo, California.**

Received 21 November 1986. Accepted 6 February 1987.

INTRODUCTION

Specimens of schizomids recently collected in Monterey County, California proved to be undescribed. This discovery is significant in that it increases the number of described species to seven for California and 10 for the continental United States, and represents the northernmost record of schizomids in the Coast Ranges of North America. *Schizomus briggsi* (Rowland, 1972), found in the Sierra Nevada of California, is the northernmost record for the order in the New World (Hom 1967; Rowland 1972*a*) and occurs only slightly further north latitudinally than this new schizomid.

Five specimens (one male, one female, and three juveniles) were collected by turning over much granitic talus in a moist, lush oak canyon in the northern Santa Lucia Range. This schizomid population was fairly restricted to cliff talus; a thorough search just outside of this zone yielded only one additional juvenile specimen. Collecting to the south of this location (near the town of Jolon) failed to yield schizomids until suitable habitats in the vicinity of San Luis Obispo, San Luis Obispo County were carefully investigated. Specimens found in these locations established new northern records for *Schizomus belkini* (McDonald and Hogue, 1957).

METHODS AND DEPOSITION

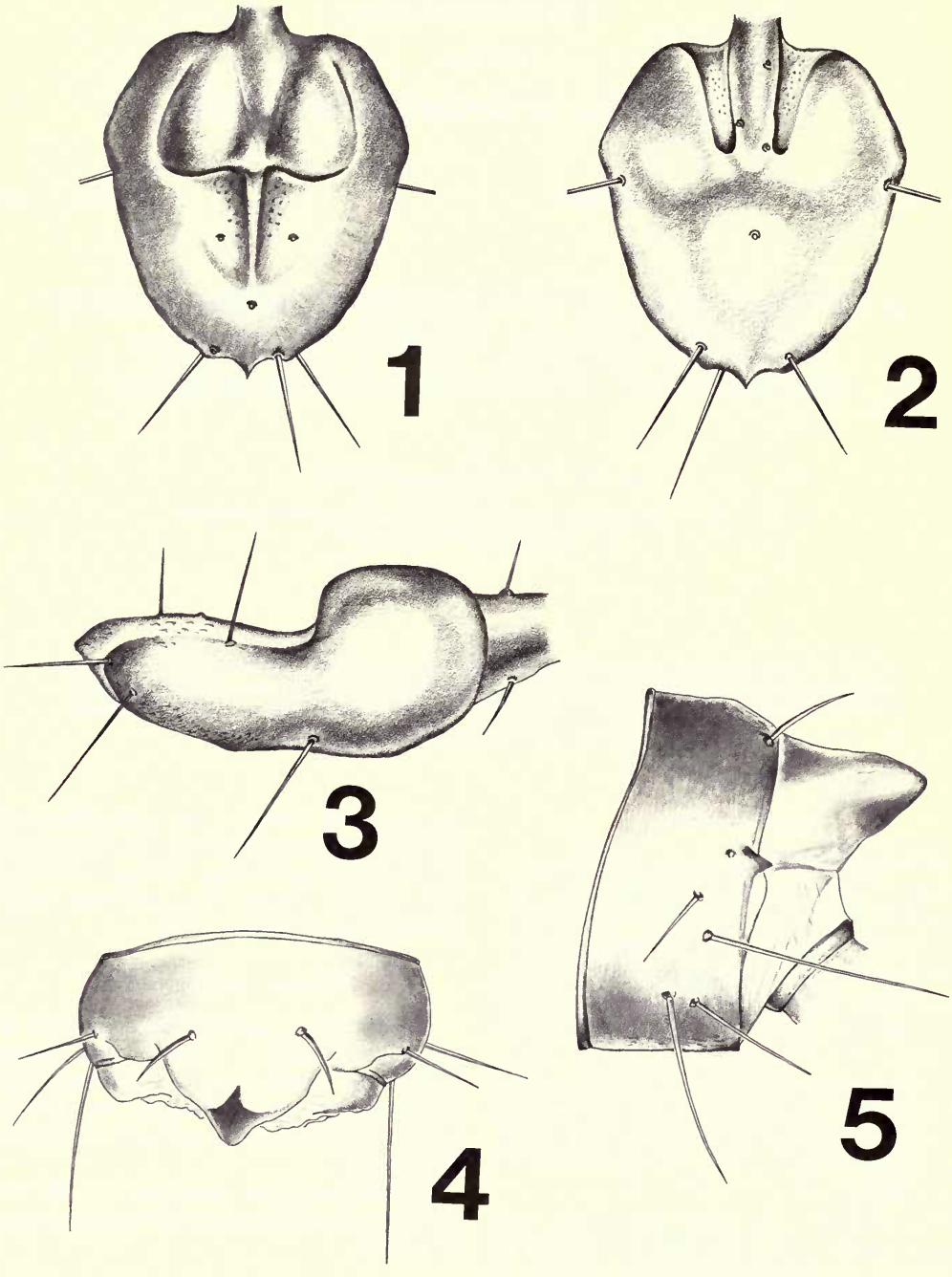
The characters used in this description are mostly those used by Rowland and Reddell (1979). The genital sternites of females were withdrawn from the opisthosoma with a thin pin, cleaned with KOH, and examined in an aqueous slide mount.

All specimens were preserved in 75% ethyl alcohol and deposited in the California Academy of Sciences.

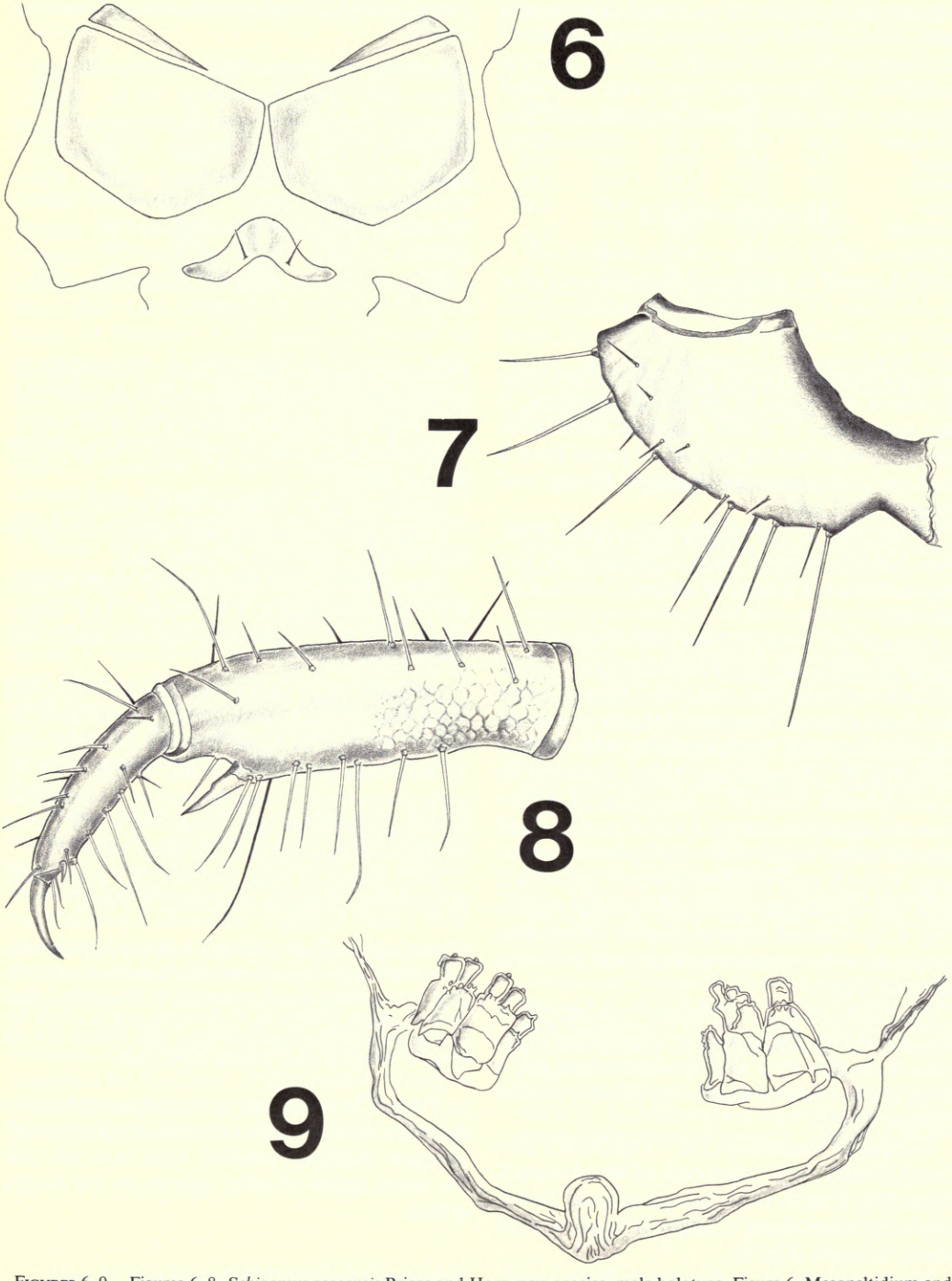
TAXONOMIC SECTION

Schizomus secoensis new species
(Figures 1–9)

DIAGNOSIS.—This species belongs to the *briggsi* group of Rowland and Reddell (1981) (=*belkini*



FIGURES 1–5. *Schizomus secoensis* Briggs and Hom, new species, male holotype. Figure 1. Dorsal view of flagellum. Figure 2. Ventral view of flagellum. Figure 3. Lateral view of flagellum. Figure 4. Dorsal view of segment XII. Figure 5. Lateral view of segment XII.



FIGURES 6–9. Figures 6–8. *Schizomus secoensis* Briggs and Hom, new species, male holotype. Figure 6. Mesopeltidium and metapeltidium. Figure 7. Ectal view of pedipalpal trochanter. Figure 8. Ectal view of pedipalpal tibia. Figure 9. Female spermathecae of *Schizomus secoensis*.

TABLE 1. MALE APPENDAGE MEASUREMENTS IN MILLIMETERS.

	I	II	III	IV	Pedipalp
Trochanter	0.30	0.20	0.20	0.33	0.33
Femur	1.17	0.83	0.73	1.07	0.50
Patella	1.43	1.17	0.33	0.43	0.63
Tibia	1.07	0.50	0.40	0.83	0.50
Basitarsus	0.37	0.50	0.50	0.73	0.33
Tarsus	0.57	0.43	0.43	0.43	
Total	4.91	3.63	2.59	3.82	2.29

TABLE 2. FEMALE APPENDAGE MEASUREMENTS IN MILLIMETERS.

	I	II	III	IV	Pedipalp
Trochanter	0.33	0.17	0.17	0.33	0.33
Femur	1.13	0.80	0.69	1.13	0.53
Patella	1.33	0.47	0.40	0.53	0.51
Tibia	1.00	0.53	0.44	0.84	0.40
Basitarsus	0.36	0.47	0.48	0.69	0.25
Tarsus	0.53	0.40	0.40	0.47	
Total	4.68	2.84	2.58	3.99	2.02

group of Rowland 1972*a, b*). It differs from other species of the group by its unique flagellum. It also has 2 pairs of dorsal prosomal setae while the other members of the *briggsi* group have 3 pairs or (*Schizomus shoshonensis* (Briggs and Hom)) only 1 pair.

ETYMOLOGY.—The specific name refers to the type locality (Arroyo Seco Campground, Los Padres National Forest, Monterey County, California).

DESCRIPTION.—*Male.* Color pale brownish with a grayish-green tint that disappeared after a year in alcohol storage. Prosoma with 2 pairs of dorsal and 3 apical setae. Eyespots elongate and indistinctly delineated. Metapeltidium with definite split (Fig. 6). Mesopeltidial plates separated by approximately width of 1 plate (Fig. 6). Abdomen not attenuated, terga I and II with 4 small anterior setae, terga I–VII with 2 posterior setae, terga VIII–IX with 4 posterior setae, tergum XII with well-developed, acute posterodorsal process (Fig. 4, 5). Vestigial stigmata slightly darker than sterna. Anterior sternum with 15 setae, posterior sternum with 6.

Flagellum (Fig. 1–3) roughly pentagonal or hexagonal with dorsal median longitudinal ridge flanked mesally by 2 shallow depressions and a basal median furrow flanked by 2 large, distinct median lobes.

Pedipalpal trochanter (Fig. 7) uniformly produced distally, without process on mesal margin. Tibia (Fig. 8) with mesal subapical spur. Tarsal-basitarsal spurs about ⅙ length of segment, claw about ⅓ length (Fig. 8).

Measurements (in millimeters): Body length, 4.37; prosoma length, 1.17, width, 0.70; flagellum length (to opisthosoma), 0.50, width, 0.43. Appendage measurements listed in Table 1.

Female. Color brown with grayish-green tinge. Prosoma similar to that of male. Abdominal setation similar to that of male except anterior sternum with 16 setae and posterior sternum with 5.

Spermathecae (Fig. 9) with 5 or 6 lobes joined at their bases.

Flagellum bears 13 setae on 4 articles.

Pedipalpal morphology and setation similar to that of male, but without tibial spur.

Measurements (in millimeters): Body length, 4.47; prosoma length, 1.15, width, 0.63; flagellum length, 0.35. Appendage measurements listed in Table 2.

Juveniles. Color pale brown with grayish-green tinge. Male juvenile with partially developed flagellum bearing 13 setae; anterior sternum with 16 setae and posterior sternum with 6. Two female juveniles with flagella bearing 13 setae and posterior sterna bearing 5 setae, one with 13 setae on anterior sternum and the other with 17.

Body length of male juvenile, 3.7 mm; body length of both female juveniles, 3.5 mm.

MATERIAL EXAMINED.—Holotype male and one male juvenile: California: Monterey County, Los Padres National Forest, west side of Arroyo Seco Campground at The Lakes, 3 April 1985, T. Briggs, T. Ohsumi, W. Rauscher, and D. Ubick. Female paratype and two female juveniles: same locality, 22 April 1986, T. Briggs, A. Jung, J. Jung, and K. Hom.

Notes. The pedipalps are not elongated in the holotype and the male juvenile, but males with elongate pedipalps possibly exist as is the case for some males of other species in the *briggsi* group.

Schizomus belkini (McDonald and Hogue)

Trithyreus belkini McDonald and Hogue, 1957:1–7; Briggs and Hom 1966:270, 273–274; Hom 1967:216–220; Rowland 1971:304, 308–309; Briggs and Hom 1972:2; Rowland 1972*a*: 1, 4, 5, 7, 8; Rowland 1972*b*:153, 155, 156, 158, 159.

Schizomus belkini: Rowland and Reddell, 1979:162; Bennett, 1985:321.

New Records.—California: San Luis Obispo County: 7.3 mi w. Pozo, 3 April 1985, under serpentine in oak-digger pine chaparral, T. Briggs, T. Ohsumi, W. Rauscher, and D. Ubick (6 females, 1 male, 4 juveniles); 1 mi e. Highway 41 on Old Morro Road, 3 April 1985, under serpentine on oak-grassland slope, T. Briggs, T. Ohsumi, W. Rauscher, and D. Ubick (2 females, 1 male, 1 juvenile); 5.3 mi w. of Los Osos Valley Road (San Luis Obispo) on Prefumo Canyon Road, 14 February 1987, under serpentine on grassland slope, T. Briggs and V. F. Lee (1 male, 1 female); 1.2 mi e. Highway 1 (Morro Bay) on Toro Creek Road, 14 February 1987, under serpentine on grassland, T. Briggs and V. F. Lee (2 males, 3 females); 2.6 mi n. Highway 1 (near Cayucos) on Thunder Canyon Road, 14 February 1987, under serpentine on grassland slope, T. Briggs and V. F. Lee (1 male with elongate pedipalps, 1 female, 1 female juvenile).

Notes. The 2 male specimens from these localities have the same shape of flagellum as the typical *S. belkini* but with slightly more prominent relief on the dorsum of the flagellum. In other respects the specimens resemble topotypical examples of *S. belkini.* Females have the four separate spermathecal lobes of typical female *S. belkini.*

Distributional Notes.—These new records require that the dispersal theory for the biogeography of Schizomida in California and Arizona proposed by Rowland (1972*b*) be revised for central California. Rowland suggested that a Pliocene embayment, extending to the San Joaquin Valley, provided a barrier preventing the northward dispersal of schizomids along the coast. This is no longer likely due to the discovery of *S. secoensis* and *S. belkini* north of that barrier. As suggested by Rowland, if this barrier could be crossed by schizomids, then the San Rafael and Santa Lucia mountains to the north should contain suitable habitats. Vicariance biogeography could just as well explain the distribution of these schizomids. The original range of an ancestral form may have been fragmented by geological and climatological changes that led to eventual speciation.

Acknowledgments

The authors are very grateful to the collectors who gave field assistance and to Karen J. Hom for illustrating the specimens. We also wish to thank James C. Cokendolpher, Texas Tech University, and Dr. Wojciech J. Pulawski and Vincent F. Lee, California Academy of Sciences, for critically reading the manuscript.

Literature Cited

Bennett, S. G. 1985. A new record of a short-tailed whip scorpion from Santa Catalina Island, California (Schizomida: Schizomidae). Pan-Pac. Entomol. 61:321–322.

Briggs, T. S. and K. Hom. 1966. A new schizomid whip-scorpion from California with notes on the others (Uropygi: Schizomidae). Pan-Pac. Entomol. 42:270–274.

———. 1972. A cavernicolous whip-scorpion from the northern Mojave Desert, California (Schizomida: Schizomidae). Occas. Pap. Calif. Acad. Sci. 98:1–7.

Hom, K. 1967. Notes on two California whip-scorpions (Uropygi, Schizomidae). Pan-Pac. Entomol. 43:216–220.

McDonald, W. A. and C. L. Hogue. 1957. A new *Trithyreus* from southern California (Pedipalpida, Schizomidae). Am. Mus. Novit. 1834:1–7.

Rowland, J. M. 1971. A new *Trithyreus* from a desert oasis in southern California (Arachnida: Schizomida: Schizomidae). Pan-Pac. Entomol. 47:304–309.

———. 1972*a*. A new species of Schizomida (Arachnida) from California. Occas. Pap. Mus. Texas Tech Univ. 5:1–9.

———. 1972*b*. Origins and distribution of two species groups of Schizomida (Arachnida). Southwest. Nat. 17:153–160.

Rowland, J. M. and J. R. Reddell. 1979. The order Schizomida (Arachnida) in the New World. I. Protoschizomidae and *dumitrescoae* group (Schizomidae: *Schizomus*). J. Arachnol. 6:161–196.

———. 1981. The order Schizomida (Arachnida) in the New World. IV. *Goodnightorum* and *briggsi* groups and unplaced species (Schizomidae: *Schizomus*). J. Arachnol. 9:19–46.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 5, pp. 89-96, 4 figs. February 5, 1988

EUCRYPHYCUS, A NEW GENUS OF CALIFORNIA EELPOUT (TELEOSTEI: ZOARCIDAE) BASED ON *MAYNEA CALIFORNICA* STARKS AND MANN, 1911

By

M. Eric Anderson

Department of Ichthyology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

ABSTRACT: The composition of *Maynea* Cunningham, 1871 has had a confused history and formerly included species currently recognized in five genera. Herein, *Maynea* is considered monotypic, including only the littoral Magellanic *M. puncta* (Jenyns, 1842), which is redescribed. The confusion stems from earlier work uniting eelpouts without pelvic fins while emphasizing overall similarity based on symplesiomorphies. The genus *Eucryphycus* is erected for the persimmon eelpout, *E. californicus* (Starks and Mann, 1911), on the basis of a combination of character states that ally it as a primitive sister taxon with *Lycenchelys* Gill, 1884, and relatives. These character states include features of the palatal arch, hyoid bar, suspensorium, occipital (supratemporal) commissure, gill slit, and suborbital bone chain.

Eucryphycus californicus is a deep-dwelling, coastal species that occurs over mud bottoms and hides in patches of decaying vegetation where it feeds primarily on gammaridean amphipods. Nesting probably occurs in this habitat as well. *Maynea puncta,* on the other hand, primarily occurs in the rocky intertidal zone and kelp stands and is most closely related to a group of nine endemic, Magellanic genera.

Received February 2, 1987. Accepted June 2, 1987.

INTRODUCTION

Cunningham (1871) established the genus *Maynea* for a littoral eelpout species (*M. patagonica*) of the "Magellan Province," or cold-temperate South America (Regan 1914; Briggs 1974). Membership of the genus has had a confused history. Species currently recognized in *Bothrocara* Bean, 1890, *Gymnelopsis* Soldatov, 1922, *Oidiphorus* McAllister and Rees, 1964, *Pachycara* Zugmayer, 1911, and another presently unnamed (based on "*Melanostigma*" *microphthalmus*), have been formerly assigned to *Maynea.* This confusion stemmed from an artificial lumping of species without pelvic fins and overemphasis of plesiomorphic characters, and, as currently constructed, the genus is monotypic (Anderson 1984*a*). Confusion has persisted with regard to the name of the South American species, originally given by Cunningham (1871) as *Maynea patagonica.* Jordan and Davis (1891) indicated this species was identical with *Conger punctus* Jenyns, 1842. I have examined Jenyns's holotype and concur that Jordan and Davis's overlooked nomenclature (*Maynea puncta* [Jenyns, 1842]) for the species is correct. Gosztonyi (1977) briefly redescribed the species (using the name *M. patagonica*), on the basis of four specimens.

C. H. Gilbert discovered a unique eelpout specimen among the 1904 California collections of the U.S. Fish Commission from 419 to 545 m off San Nicolas Island. Thinking his species was related to the South American form, Gilbert

prepared a new species description for his specimen, naming it *Maynea californica,* but publication was somewhat delayed (Gilbert 1915). Meanwhile, Starks and Mann (1911) used Gilbert's name and gave a brief description of the species. Following Article 50(a) of the International Code of Zoological Nomenclature, the authorship of *M. californica* must be attributed to Starks and Mann (Hubbs et al. 1979).

Most references to *M. californica* have been limited to brief descriptions or citations in checklists and keys, and all have incorrectly given Gilbert (1915) when citing authorship (Jordan et al. 1930; Barnhart 1936; McAllister and Rees 1964; Fitch and Lavenberg 1968; Eschmeyer et al. 1983). Cailliet and Lea (1977) provided detailed information on the biology and distribution of *M. californica* based on over 1,200 specimens caught in Monterey Bay between 1972 and 1975. These specimens formed the basis of an unpublished master's thesis (Kliever 1976), which provided a more complete description of the submarine canyon habitat and biology of *M. californica* than that given by Cailliet and Lea (1977). A comparative anatomical study of *Maynea* and putative sister taxa revealed major osteological differences between *M. puncta* and *M. californica* (see Anderson, 1984*a*).

The purpose of this paper is to erect a new genus for *M. californica* and redescribe it and the monotypic *M. puncta* on the basis of recently collected material. My earlier methodology (Anderson 1982, 1984*a*) is used to establish a detailed anatomical basis from which other problematical southern hemisphere zoarcid genera may be discussed in the future.

Methods and Materials

Measurements were made with an ocular micrometer or dial calipers to the nearest 0.1 mm. Osteological observations were made on cleared and stained specimens (Dingerkus and Uhler 1977) and drawings made with the aid of a camera lucida. Definitions of characters and measurements follow those of Gosztonyi (1977) and Anderson (1982, 1984*a*). Character state modifiers are based on those numerically scored characters of Anderson (1984*a*). Museum abbreviations follow Leviton et al. (1985).

The following specimens were examined in detail; counts were taken from radiographs of all known specimens of *Maynea puncta,* 30 specimens of *Eucryphycus californicus* from CAS 38674, and all specimens of *E. californicus* from VIMS 05806. Measurements are in standard length (SL).

Maynea puncta

BMNH 1869.5.3.25 (holotype of *M. patagonica*; 153 mm); Otter Isl., Straits of Magellan, Chile; Magellan Survey, 1867–1869. BMNH 1917.7.14.12 (holotype of *Conger punctus*; 78 mm); Beagle Channel, Tierra del Fuego; Charles Darwin, 1833. VIMS 05783 (1; 149 mm, cleared and stained); Ushuaia, Argentina; intertidal coll., A. Gosztonyi; 23 Nov. 1968. AMNH 5016 (1; 139 mm); Argentina, no specifics; shore coll.; 1900. LACM 10722-1 (1; 250 mm); Isla Desolación, Chile; 52°56′S, 75°00′W; ELTANIN sta. 958; 92–101 m; 5 Feb. 1964. LACM 10724-1 (1; 78 mm); Straits of Magellan, Chile; 52°40′S, 74°58′W; ELTANIN sta. 960; 64 m; 6 Feb. 1964. LACM 43712-1 (1; 29.5 mm); Isla de los Estados (Staten Isl.), Argentina; 54°55′S, 64°00′W; HERO sta. 875; 0–903 m (surface capture?); 27 Oct. 1971. LACM 43713-1 (8; 62–123 mm); Isla Dawson, Chile; 53°51′32″S, 70°25′52″W; USARP shore coll., sta. 69-24; 1.5–3.0 m; 18 May 1969. LACM 43723-1 (1; 115 mm); Punta Santa Ana, Penin. de Brunswick, Chile; 53°30′48″S, 70°50′33″W; USARP shore coll., sta. 69-9A; 0.3–0.6 m; 16 Apr. 1969. LACM 43728-1 (1; 92 mm); Isla de los Estados, Argentina; 54°53.7′S, 65°27.4′W; HERO sta. 689; 12–13 m; 15 Oct. 1971. MACN 1847 (3; 57–114 mm); Isla de los Estados, Argentina; SAN LUIS. MACN 2686 (1; 198 mm); off Ushuaia, Argentina; BAHIA BLANCA; 17 Apr. 1941. SIO 74-109 (1; 76 mm); Merle Cove, Argentina; 54°47.8′S, 64°00.5′W; kelp bed; 9 May 1973.

Eucryphycus californicus
(all Monterey Bay specimens studied are from area centering on 36°48′N, 121°48′W in 130–143 m)

SU 22399 (paratype; 85 mm); off San Diego; San Diego Biological Association; 1907–1911. VIMS 05806 (16; 48–173 mm, cleared and stained); Monterey Bay. CAS 17623 (7; 35–184 mm); Monterey Bay. CAS 38674 (52; 66–200 mm SL); Monterey Bay. CAS 38711 (19; 75–225

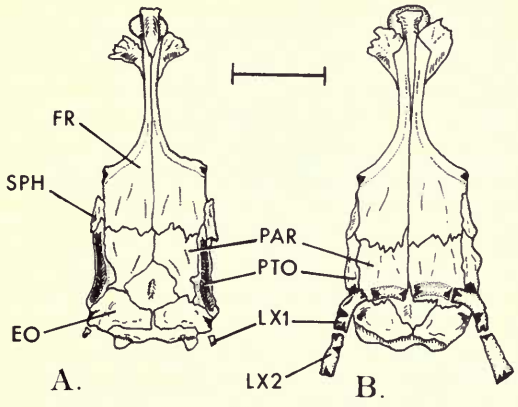


FIGURE 1. Dorsal view of neurocrania of A) *Maynea puncta,* VIMS 05783, 149 mm SL, and B) *Eucryphycus californicus,* VIMS 05806, 173 mm SL. Abbreviations: EO, epioccipital; FR, frontal; LX1, first and LX2, second, lateral extrascapulars; PAR, parietal; SPH, sphenotic.

mm); Monterey Bay. CAS 39572 (1; 92 mm); off Pt. Conception; 34°22.4'N, 120°25.8'W; VELERO IV sta. 25875; 183 m; 20 Mar. 1977.

Maynea Cunningham, 1871

(Figures 1A, 2A, 3A, 4A)

Maynea Cunningham, 1871:471, 472 (type species: *Maynea patagonica* Cunningham, 1871 [=*Conger punctus* Jenyns, 1842], by monotypy); Günther 1881:20, pl. II, fig. C, D; Jordan and Davis 1891:663; Lahille 1908: 438, 439, fig. 8; Norman 1937:108; McAllister and Rees 1964:105–108 (partim); Gosztonyi 1977:220–223, fig. 12.

DIAGNOSIS.—Palatal arch well developed, with ectopterygoid and mesopterygoid overlapping half or more dorsal and anterior margins of quadrate; ceratohyal-epihyal juncture with bone interdigitating; hyomandibular posterior ramus elongate; five branchiostegal rays; gill slit restricted, extending ventrally to midpectoral base or above it; vertebrae 27–31 + 87–100 = 117–130; occipital (supratemporal) commissure and bony passage in parietals absent; one lateral extrascapular; two postorbital pores; eight suborbital bones; with six suborbital pores.

Maynea puncta (Jenyns, 1842)

DIAGNOSIS.—As for genus.

COUNTS AND MEASUREMENTS.—Vertebrae 27–31 + 87–100 = 117–130; D 116–129; A 91–105; P 13–16; pelvics absent; C 6–10; pseudobranch filaments 3–5; gill rakers 1–3 + 8–11 = 9–13; branchiostegal rays 5; vomerine teeth 0–4; palatine teeth 1–4; premaxillary teeth 6–13; dentary teeth 7–17. Following measurements in percent SL: head length 12.6–17.9; predorsal length 11.8–16.0; preanal length 34.0–39.8; body height 6.9–9.4; pectoral fin length 6.4–9.8; caudal fin length 0.7–1.5. Following measurements in percent HL: head width 38.4–67.8; upper jaw length 34.2–45.2; pectoral fin length 47.3–58.8; body height 47.2–68.4; snout length 17.0–23.6; eye diameter 19.9–27.7; gill slit length 18.7–27.1; interorbital width 8.3–12.8; interpupillary width 18.6–23.4. Pectoral base/length ratio 39.8–56.0.

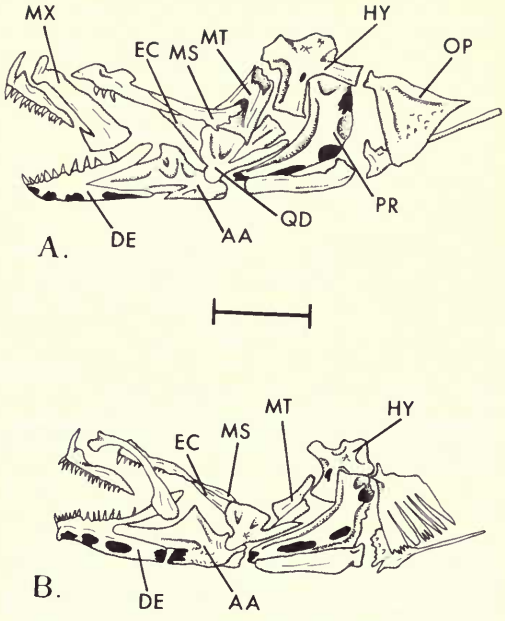


FIGURE 2. Left lateral view of jaws, suspensoria and opercular bones of A) *Maynea puncta,* VIMS 05783, 149 mm SL, and B) *Eucryphycus californicus,* VIMS 05806, 173 mm SL. Abbreviations: AA, anguloarticular; DE, dentary; EC, ectopterygoid; HY, hyomandibula; MS, mesopterygoid; MT, metapterygoid; MX, maxilla; OP, opercle; PR, preopercle; QD, quadrate.

DESCRIPTION.—Head relatively small, ovoid, juveniles with more rounded snout and relatively larger eye than adults. Widest portion of head midway between eye and gill opening, but sexual dimorphism in head length or width not statistically detected in present sample ($n = 21$), owing to predominance of juveniles. Late juveniles and adults with head length 12.6–15.5% SL; 29.5 mm hatchling with head length 17.9% SL. Body relatively elongate, laterally compressed, but this less pronounced in largest adults. Tail greatly elongated, increasingly laterally compressed posteriad. Skin firm, covering vertical fins. Scales minute, cycloid, imbedded, covering body (ex-

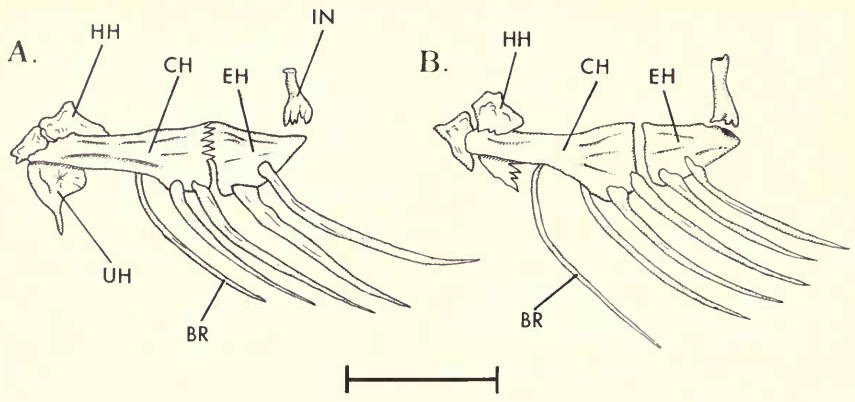


FIGURE 3. Left lateral view of hyoid bars of A) *Maynea puncta,* VIMS 05783, 149 mm SL, and B) *Eucryphycus californicus,* VIMS 05806, 173 mm SL. Abbreviations: BR, branchiostegal ray; CH, ceratohyal; EH, epihyal; HH, hypohyal (dorsal); IN, interhyal; UH, urohyal.

cept on ventral surface of abdomen) and tail, including vertical fins; scales absent on head and nape. No scales in 29.5-mm SL hatchling, and those on body of next largest specimen (57 mm SL) extend in wedge-shaped pattern anteriorly from vertical through anus to gill opening. Lateral line mediolateral (Andriashev 1954), complete, extending from just posterior fourth postorbital pore to tail tip, not bowed anteriorly. Eye moderate, rounded in juveniles, somewhat ovoid in largest adults; eye longer in relation to head in juveniles than adults. Nostrils single, at snout tip, nasal tube not reaching upper lip. Pectoral fin moderately large, posterior margin evenly rounded, its origin just ventral to body midline; pectoral base extending ventrally to abdomen; middle rays longest, ventralmost not thickened or excised at tips; juveniles with relatively longer fin than adults. Gill slit restricted, extending ventrally to midpectoral base or above (opposite pectoral rays 2–7).

Mouth terminal, lips without lobes; mouth rel-

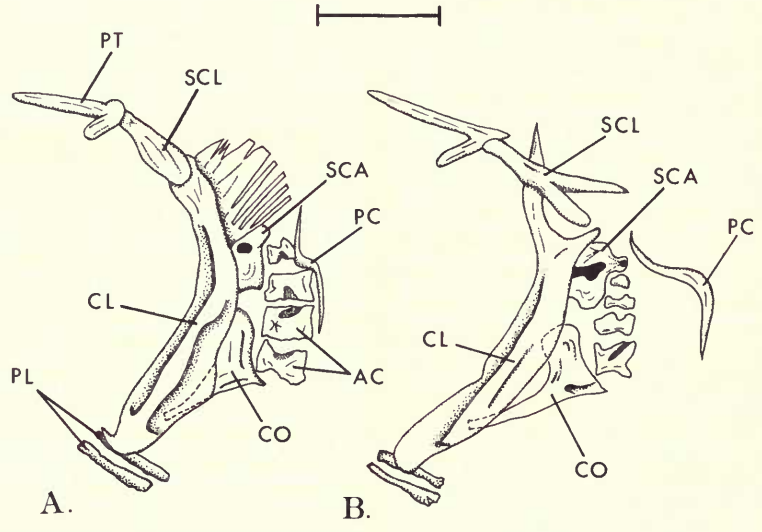


FIGURE 4. Left lateral view of pectoral girdles of A) *Maynea puncta,* VIMS 05783, 149 mm SL, and B) *Eucryphycus californicus,* VIMS 05806, 173 mm SL. Abbreviations: AC, actinost; CL, cleithrum; CO, coracoid; PC, postcleithrum; PL, pelvic bone; PT, posttemporal; SCA, scapula; SCL, supracleithrum.

atively small, upper jaw extending posteriorly to vertical through middle of eye or its posterior margin. Upper jaw length apparently sexually dimorphic, but only one adult of each sex known; largest known male (250 mm SL) with jaw 45.2% HL, largest known female (198 mm SL) with jaw 38.3% HL. Largest fish with two rows of small, conical teeth on anterior portion of both jaws, blending into single, posterior row. Outer, anterior teeth of both jaws slightly larger than innermost; no sexual dimorphism in dentition. Teeth relatively few on vomer and palatine bones.

Cephalic lateralis pores enlarged, rounded, relatively larger in smallest juveniles; pore system moderately reduced, present sample with no numeric variation in pore counts. Occipital (temporal) and interorbital pores absent. Two pairs of nasal (anterior supratemporal) pores, one set anteromesial to nasal tube, the other set posteromesial. Eight preoperculomandibular pores, four emanating from dentary, one from anguloarticular, and three from preopercle. Six suborbital pores, all emanating from ventral ramus of suborbital chain. Postorbital pores one and four present emanating from frontal (first) and lateral extrascapular (fourth). Parietal bones large, meeting in midline, with no trace of tubular canal for commissure (Fig. 1A). Supraoccipital large, widely separated from exoccipital by epioccipitals. Postorbital commissure a troughlike depression in pterotic. Single pair of small lateral extrascapulars (anteriormost) at posterolateral edge of neurocranium.

Palatal arch strong, ectopterygoid and mesopterygoid with posterior surfaces overlapping more than half anterior and dorsal margins of quadrate (Fig. 2A). Hyomandibular posterior ramus elongate. Opercle, subopercle, and metapterygoid relatively large and well ossified.

Ceratohyal-epihyal juncture with bone interdigitating dorsally (Fig. 3A). Branchiostegal rays five: three articulating with ceratohyal and two with epihyal. Ceratobranchial five dentigerous; three pairs of infrapharyngobranchials and tooth plates. Gill rakers blunt, triangular, 9–13 total; largest specimens with 3 epibranchial rakers and 10–11 on first ceratobranchial.

Posttemporal ventral ramus well developed (Fig. 4A). Supracleithrum simple, broadened at midlength. Cleithrum with dorsal, poorly ossified lamina. Scapular foramen enclosed; scapular posterior ramus moderately well developed. Single postcleithrum present. Four ossified actinosts bearing 13–16 pectoral fin rays. Pelvic fins absent, pelvic bones normal size.

Vertebrae nonequiamphicoelous (asymmetric); precaudal vertebrae usually 29 or 30, caudal vertebrae usually 96–99. Epipleural ribs on vertebrae 1–18, occasionally to vertebra 21. Pleural ribs on third through ultimate or, less often, penultimate precaudal vertebra. Dorsal fin origin associated with first, rarely second, vertebra, with no free pterygiophores. All dorsal fin elements soft rays. Two to five anal fin pterygiophores inserted anterior to haemal spine of first caudal vertebra. Last dorsal ray associated with third or fourth preural vertebra. Last anal ray associated with second preural vertebra; often two anal rays attached to its associated pterygiophore, which is fused to haemal spine. Caudal fin rays 6–10, with 1–2 (usually 2) epural rays, 3–4 upper hypural, and 2–4 (usually 3) lower hypural rays.

Palatine membrane (oral valve) well developed, overlapping anterior margin of vomer. Three to five relatively long pseudobranch filaments. Two nublike pyloric caeca, generally longer in smallest specimens.

Present collections indicate that two color morphs exist. The commoner, characteristic of specimens caught in nearshore and littoral waters, is banded. These forms have 12–16 wide brown bands extending across the body and tail onto the fins (less extensive on anal) on a pale yellowish or whitish background, and the occiput has a pale, transverse band. The other morph, characteristic of specimens taken in offshore waters, is monotone brown with gray areas on cheeks, jaws, and gill isthmus region, sometimes with light mottling on head. Pectoral fins grayish with white edges (Gosztonyi 1977).

Distribution and Habitat.—Known from inlets of southern Chile, around Tierra del Fuego and the Falkland Islands, from the intertidal zone and subtidal kelp stands to the outer continental shelf in depths to 101 m. Capture records indicate the species has no substrate preference, being taken in tidepools with varying amounts of algal cover to mud bottoms of the outer Chilean shelf. One hatchling, 29.5 mm SL (LACM 43712-1) from a Blake trawl fished at 771–903 m, probably was caught as the net surfaced, since this depth is excessive and planktonic larvae (with durations up to two weeks) are known in some eelpouts (Anderson 1984*b*).

Eucryphycus gen nov.

(Figures 1B, 2B, 3B, 4B)

Maynea (non-Cunningham, 1871). Starks and Mann 1911:16–18; Gilbert 1915:362–364, pl. 19, fig. 17; Hubbs 1916:166; Barnhart 1936:91, fig. 275; McAllister and Rees 1964:107

(partim); Cailliet and Lea 1977:253–261, fig. 1, 2; Eschmeyer et al. 1983:106, pl. 11.

TYPE SPECIES.—*Maynea californica* Starks and Mann, 1911.

DIAGNOSIS.—Palatal arch reduced, ectopterygoid and mesopterygoid not overlapping half of dorsal and anterior margins of quadrate; ceratohyal-epihyal juncture smooth; hyomandibular posterior ramus normal; six branchiostegal rays; gill slit extending below ventral margin of pectoral base; vertebrae 26–29 + 79–86 = 106–115; occipital (supratemporal) commissure well developed, with tubular passage across parietals and three occipital pores; two lateral extrascapulars; four postorbital pores; eight suborbital bones, with eight suborbital pores.

Eucryphycus californicus
(Starks and Mann, 1911)

DIAGNOSIS.—As for genus.

COUNTS AND MEASUREMENTS.—Vertebrae 26–29 + 79–86 = 106–115; D 97–108; A 82–89; P 13–15; pelvics absent; C 9–10; pseudobranch filaments 3–4; gill rakers 1–3 + 7–13 = 8–16; branchiostegal rays 6; vomerine teeth 2–11; palatine teeth 5–17; premaxillary teeth 9–27; dentary teeth 11–27. Following measurements in percent SL: head length 12.0–17.6; predorsal length 15.1–19.9; preanal length 34.8–37.6; body height 6.9–9.4; pectoral fin length 6.3–8.8; caudal fin length 2.1–4.2. Following measurements in percent HL: head width 28.6–66.7; upper jaw length 35.9–49.0; pectoral fin length 44.7–59.3; body height 39.2–77.9; snout length 15.1–18.5; eye diameter 15.9–24.3; gill slit length 30.0–35.5; interorbital width 8.0–9.6; interpupillary width 24.0–34.7. Pectoral base/length ratio 30.6–43.0.

DESCRIPTION.—Head moderately large, ovoid, early juveniles with longer heads than adults (17.1–17.6% SL at 35–42 mm SL; 12.0–15.7% SL over 60 mm SL). Adult males over 190 mm SL with longer heads (14.3–15.7% SL) than similarly sized females (12.0–13.8% SL). Widest part of head midway between eye and gill opening, but no sexual dimorphism in width detected, despite great variation noted above. Body relatively elongate, laterally compressed, but more rounded in largest adults. Tail greatly elongated, increasingly laterally compressed posteriad. Skin firm, covering vertical fins. Scales minute, cycloid, imbedded, covering body including ventral surface of abdomen and tail; scales present on vertical fins, extending on dorsal to about ¾ its height, and on anal to about ½ its height. Scales absent in 35–42 mm SL specimens; those on body of next largest (52 mm SL) reach anteriorly to just behind pectoral fin margin and extend from dorsal base to abdomen. Lateral line mediolateral (Andriashev 1954), complete, extending from just posterior to fourth postorbital pore to tail tip, not bowed anteriorly. Eye moderate, rounded in juveniles, more ovoid in largest adults; eye longer in relation to head in juveniles than adults. Nostril single, at snout tip, nasal tube just reaching upper lip. Pectoral fin moderately large, middle rays longest; juveniles with relatively longer fin than adults; posterior margin evenly rounded, its origin below body midline; pectoral base extending ventrally onto abdomen; ventralmost rays thickened and very slightly excised at tips. Gill slit extending below ventral margin of pectoral base.

Mouth terminal, lips without lobes. Mouth moderately large, upper jaw extending to vertical through posterior margin of eye in adult males, with jaw length 42.1–49.0% HL; upper jaw extending to middle of eye or slightly beyond in adult females, with jaw length 35.9–37.9% HL. All sizes and both sexes with two rows of small, conical teeth on anterior portion of premaxilla, blending into single, posterior row. Juveniles with two rows of teeth anteriorly on dentary, adults with three rows, blending into single posterior row. Outer, anterior teeth of both jaws longer and sharper in adult males than females. Teeth relatively numerous on vomer and palatine bones in adults; palatine teeth in two rows anteriorly in adults.

Cephalic lateralis pores moderately enlarged, rounded, relatively larger in smallest juveniles; pore system relatively complete, numeric variation in pore counts seen only in suborbital canal. Three occipital (temporal) pores across nape. Interorbital pore absent. Two pair of nasal (anterior supraorbital) pores, one set anteromesial to nasal tube, the other set posteromesial. Eight preoperculomandibular pores, four emanating from dentary, one from anguloarticular, and three from preopercle. Eight, rarely seven, suborbital pores, six emanating from ventral ramus of suborbital bone chain and one or two from ascending ramus (when seven pores in canal, uppermost absent). Four postorbital pores present, emanating from frontal (first), pterotic (second), between anterior and posterior lateral extrascapulars (third), and from end of posterior lateral extrascapular (fourth). Parietal bones large, meeting in midline, with well developed tubular canal, presumably representing fused tabulars, passing commissure (Fig. 1B). Supraoccipital relatively small, nearly

articulating with exoccipital. Postorbital commissure a tubular passage through frontal, sphenotic, pterotic, and extrascapulars.

Palatal arch reduced, ectopterygoid and mesopterygoid not overlapping half anterior and dorsal margins of quadrate (Fig. 2B). Hyomandibular posterior ramus not elongated. Posterior surface of opercle poorly ossified. Metapterygoid relatively small.

Ceratohyal-epihyal juncture smooth; cartilage-filled space between bones (Fig. 3B). Branchiostegal rays six: four articulating with ceratohyal and two with epihyal. Ceratobranchial five dentigerous; three pairs of infrapharyngobranchials and tooth plates. Gill rakers blunt, triangular, sharper and longer dorsally; largest specimens with 3 epibranchial rakers and 12–13 on ceratobranchial.

Posttemporal ventral ramus well developed (Fig. 4B). Supracleithrum forked at posterior end. Cleithrum without dorsal lamina. Scapular foramen enclosed; scapular posterior ramus well developed. Single postcleithrum present. Four ossified actinosts bearing 13–15 pectoral fin rays. Pelvic fins absent; pelvic bones normal size.

Precaudal vertebrae asymmetrical anteriorly, usually 27–28. Caudal vertebrae and posterior precaudals symmetrical; caudal vertebrae usually 80–84. Epipleural ribs on vertebrae 1–11, occasionally to vertebra 14. Pleural ribs on first through ultimate precaudal vertebra. Dorsal fin origin associated with vertebrae 4–6, usually with fifth, with no free pterygiophores. All dorsal fin elements soft rays. Three or four anal fin pterygiophores inserted anterior to haemal spine of first caudal vertebra. Last dorsal ray associated with third or fourth preural vertebrae. Last anal ray associated with second preural vertebra; usually two anal rays attached to its associated pterygiophore, which is fused to haemal spine. Caudal fin rays 9–10, with 2 epural rays, 4 upper hypural, and 3–4 (usually 4) lower hypural rays.

Palatine membrane weak, not reaching anterior edge of vomer. Three to four relatively long pseudobranch filaments. Two nublike pyloric caeca.

Fresh coloration uniformly dark orange, with somewhat rust-colored head. Throat region, branchiostegal membranes, and abdomen light orange (persimmon).

Distribution and Habitat.—Known from off San Diego northward to Monterey Bay, California, from 73 to 545 m. Habitat is drifting masses of decomposing seaweed, or similar refugia, which attracts its major prey, gammaridean amphipods. Both very young fish (35 mm SL) and adults have been taken in this habitat in seaweed-baited "habitat traps" (Kliever 1976; Cailliet and Lea 1977).

Etymology.—From the Greek *ευκρῦφαῖος* (well hidden) and *φῦκος* (seaweed), alluding to its habit of hiding in masses of drifting seaweeds. Gender: masculine.

Discussion

As stated earlier, membership in *Maynea,* recognized here as monotypic, has involved species currently placed in five genera. Characters used by previous workers, taken as generic-level similarities, usually have been primitive within Zoarcidae as I defined it (Anderson 1984*a*). These include gill arch features, dentition, squamation, lateral line morphology, pectoral girdle and fin architecture, and the caudal skeleton.

Maynea puncta belongs in a group of nine endemic South American genera characterized by a single synapomorphy: the interdigitating ceratohyal-epihyal articulation (Fig. 3A). Further, *Maynea* is allied with its sister genus *Phucocoetes* Jenyns, 1842, by two other synapomorphies: the elongated posterior ramus of the hyomandibula and the restricted gill opening. *Pogonolycus* Norman, 1937, placed with this group by Anderson (1984*a*) may have greater affinity with the problematical *Oidiphorus* McAllister and Rees, 1964 (Anderson in prep.).

Eucryphycus belongs in a group of seven widely distributed deep-sea genera characterized by a great attenuation of the body and tail, with concomitant vertebral increase, head-pore enlargement, and palatal-arch reduction. This group includes *Lycenchelys* Gill, 1884; *Lycodonus* Goode and Bean, 1883; and similar species groups. Phylogeny within these groups has not been demonstrated and generic relationships are still unclear because of the current rarity of specimens in museums and incomplete knowledge of their anatomy, as well as the homoplasious distribution of major features of the group (Anderson 1984*a*, fig. 15). Nevertheless, it is clear that *Maynea* and allies sprang from a lineage distinct from that of *Eucryphycus* and its allies.

Acknowledgments

This study is dedicated to the memory of the late Ed O'Connor, fellow student and *Eucryphycus* stalker, who helped kindle in me an interest in eelpouts and other fishy things during the early

days of our studies at Moss Landing Marine Laboratories. It was Ed who convinced me to take part in the December 1972 cruise that captured the first Monterey Bay *Eucryphycus* reported by Cailliet and Lea (1977). A great deal of appreciation and thanks over the years on this and other projects is owed to Greg Cailliet and Bob Lea.

Literature Cited

Anderson, M. E. 1982. Revision of the fish genera *Gymnelus* Reinhardt and *Gymnelopsis* Soldatov (Zoarcidae), with two new species and comparative osteology of *Gymnelus viridis*. Natl. Mus. Nat. Sci., Publ. Zool. 17:1–76.

———. 1984*a*. On the anatomy and phylogeny of the Zoarcidae (Teleostei: Perciformes). Ph.D. Dissertation, College of William and Mary, Williamsburg, Virginia. 254 pp.

———. 1984*b*. Zoarcidae: development and relationships. Pp. 578–582 *in* Ontogeny and systematics of fishes. H. G. Moser et al., eds. Spec. Publ. Am. Soc. Ichthyol. Herpetol. 1:578–582.

Andriashev, A. P. 1954. Fishes of the northern seas of the USSR. Zool. Inst., Acad. Sci., Contr. Fauna USSR 53:1–566.

Barnhart, P. S. 1936. Marine fishes of southern California. University of California Press, Berkeley, California. 209 pp.

Bean, T. H. 1890. New fishes collected off the coast of Alaska and the adjacent region southward. Proc. U.S. Natl. Mus. 13:37–45.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill Co., New York, New York. 475 pp.

Cailliet, G. M. and R. N. Lea. 1977. Abundance of the "rare" zoarcid, *Maynea californica* Gilbert, 1915, in the Monterey Canyon, Monterey Bay, California. Calif. Fish Game 63(4):253–261.

Cunningham, R. O. 1871. Notes on the reptiles, amphibia, fishes, mollusca and crustacea obtained during the voyage of H.M.S. "Nassau" in the years 1866–69. Trans. Roy. Soc. London 27(4):465–502.

Dingerkus, G. and L. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Tech. 52(4):229–232.

Eschmeyer, W. N., E. S. Herald, and H. Hammann. 1983. A field guide to Pacific coast fishes of North America. Houghton-Mifflin Co., Boston, Massachusetts. 336 pp.

Fitch, J. E. and R. J. Lavenberg. 1968. Deep water teleostean fishes of California. University of California Press, Berkeley, California. 155 pp.

Gilbert, C. H. 1915. Fishes collected by the United States fisheries steamer "Albatross" in southern California in 1904. Proc. U.S. Natl. Mus. 48:305–380.

Gill, T. N. 1884. On the anacanthine fishes. Proc. Acad. Nat. Sci., Philadelphia:167–183.

Goode, G. B. and T. H. Bean. 1883. Reports on the results of dredging under the supervision of Alexander Agassiz, on the east coast of the United States, during the summer of 1880, by the Coast Survey steamer "Blake," Commander J. R. Bartlett, U.S.N., commanding. XIX. Report on the fishes. Bull. Mus. Comp. Zool. 10(5):183–226.

Gosztonyi, A. E. 1977. Results of the research cruises of FRV "Walther Herwig" to South America. XLVIII. Revision of the South American Zoarcidae (Osteichthyes, Blennioidei), with the description of three new genera and five new species. Arch. FischWiss. 27(3):191–249.

Günther, A. 1881. Account of the zoological collection made during the survey of H.M.S. "Albert" in the Straits of Magellan. Proc. Zool. Soc. London:1–141.

Hubbs, C. L. 1916. Notes on the marine fishes of California. Univ. Calif. Publ. Zool. 16(13):153–169.

Hubbs, C. L., W. I. Follett, and L. J. Dempster. 1979. List of the fishes of California. Occ. Pap. Calif. Acad. Sci. 133: 1–51.

Jenyns, L. 1842. The zoology of the voyage of H.M.S. Beagle, under the command of Captain Fitzroy, R.N. during the years 1832 to 1836. IV. Fish. Smith, Elder and Co., London. 172 pp.

Jordan, D. S. and B. M. Davis. 1891. A preliminary review of the apodal fishes or eels inhabiting the waters of America and Europe. Rept. U.S. Comm. Fish. 16:581–677.

Jordan, D. S., B. W. Evermann, and H. W. Clark. 1930. Checklist of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Rept. U.S. Comm. Fish. (1928), part II:1–670.

Kliever, R. G. 1976. Natural history of *Maynea californica* (Pisces: Zoarcidae) in a drift seaweed habitat in the Monterey Submarine Canyon, Monterey Bay, California. M.A. Thesis, California State University, San Jose, California. 70 pp.

Lahille, F. 1908. Nota sobre los zoarcidos Argentinos. Ann. Mus. Nac. Buenos Aires, ser. 3. 9:403–441.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, and C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985(3):802–832.

McAllister, D. E. and E. I. S. Rees. 1964. A revision of the eelpout genus *Melanostigma*, with a new genus and with comments on *Maynea*. Natl. Mus. Canada, Bull. 199:85–109.

Norman, J. R. 1937. Coast fishes, II, The Patagonian region. Discovery Rept. 16:1–150.

Regan, C. T. 1914. Fishes. Brit. Antarc. ("Terra Nova") Exped., 1910, Zool. 1(1):1–54.

Soldatov, V. K. 1922. On a new genus and three new species of Zoarcidae. Ann. Mus. Zool., Acad. Sci. USSR 27:159–163.

Starks, E. C. and W. M. Mann. 1911. New and rare fishes from southern California. Univ. Calif. Publ. Zool. 8(2):9–19.

Zugmayer, E. 1911. Diagnoses des poissons nouveaux provenant des campagnes du yacht "Princesse-Alice" (1901–1910). Bol. Inst. Oceanogr., Monaco (193):1–14.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 6, pp. 97-102, 2 figs. February 5, 1988

A NEW LATE EOCENE SPECIES OF PLOTOPTERIDAE (AVES: PELECANIFORMES) FROM NORTHWESTERN OREGON

By

James L. Goedert

15207 84th Ave. Ct. NW, Gig Harbor, Washington 98335 and
Museum Associate, Section of Vertebrate Paleontology,
Natural History Museum of Los Angeles County,
900 Exposition Boulevard, Los Angeles, California 90007

ABSTRACT: A new genus and species of penguin-like pelecaniform bird, *Phocavis maritimus*, is represented by a single right tarsometatarsus. This fossil is from the deep-water sediments of the Late Eocene age Keasey Formation in northwestern Oregon and is the oldest known member of the extinct family Plotopteridae.

Submitted 20 June 1986. Accepted 11 February 1987.

INTRODUCTION

A recently discovered tarsometatarsus from the Late Eocene age Keasey Formation of northwestern Oregon (Fig. 1) represents the oldest known member of the family Plotopteridae and is the first record of a plotopterid from rocks in Oregon. The first species of the family to be recognized was *Plotopterum joaquinensis* Howard, 1969, based on the scapular end of a left coracoid from the Early Miocene age Pyramid Hill Sand Member of the Jewett Sand in Kern County, California. Howard erected a new family, the Plotopteridae, for this penguin-like pelecaniform bird. Unnamed specimens of Late Oligocene and Early Miocene age from Japan, some of which include tarsometatarsi, have been discussed and figured by Hasegawa et al. (1979), and the family was reviewed by Olson and Hasegawa (1979). Another plotopterid, *Tonsala hildegardae* Olson, 1980, was described from a partial skeleton that was collected from the Oligocene and Early Miocene age Pysht Formation in northwestern Washington. The most detailed diagnosis of the Plotopteridae was presented by Olson (1980). An isolated femur from Middle Miocene age rocks in Japan, originally referred, questionably, to the Phalacrocoracidae (Hasegawa et al. 1977) has been assigned to the genus *Plotopterum* by Olson and Hasegawa (1985). Other undescribed plotopterids have been mentioned by Olson (1985) in a recent summary of the fossil record of the Plotopteridae.

The specimen described here cannot be directly compared to *Plotopterum joaquinensis* or *Tonsala hildegardae* until the tarsometatarsi of these species are found. The unnamed specimen from Kyushu, Japan (Hasegawa et al. 1979) includes the only previously described plotopterid tarsometatarsus. Current knowledge of the morphology of the leg in the Plotopteridae is, however, sufficient (Hasegawa et al. 1979; Olson and Hasegawa 1979, 1985; Olson 1980, 1985) to establish the familial allocation of the new genus and species.

Avian skeletal terminology used here follows

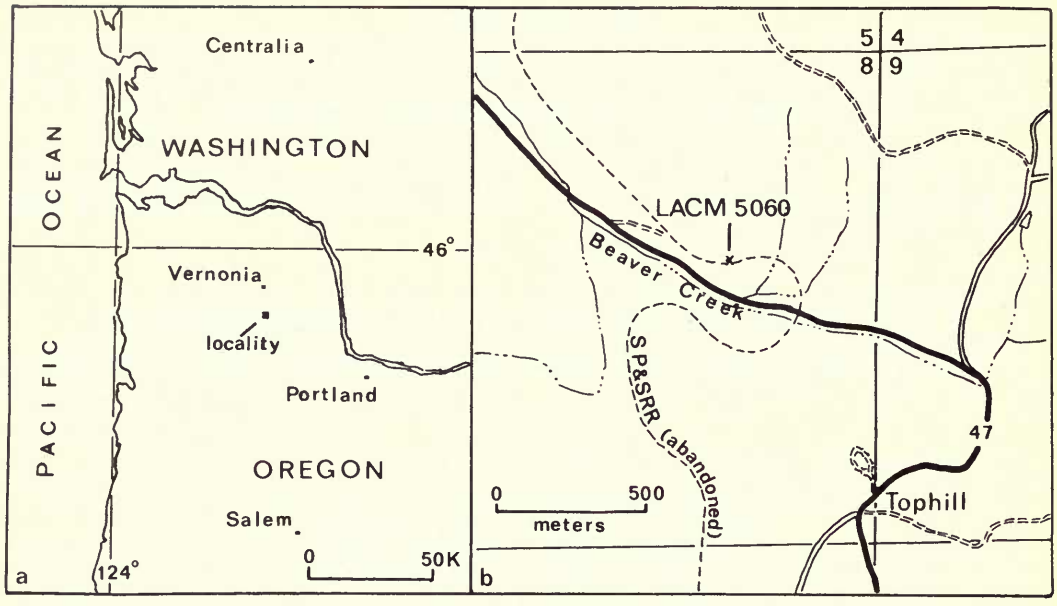


FIGURE 1. Location map. (*a*) Map of southwest Washington and northwest Oregon showing location of *b*; (*b*) type locality, LACM 5060 (Vernonia Quadrangle, 1979 edition).

that of Howard (1929). The repository for the holotype is the Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A., and is abbreviated LACM. The specimen described here was found with the distal end protruding from a small, extremely hard concretion, and was initially prepared by etching with dilute acetic acid. The remaining matrix was removed with an air abrasive unit. The specimen is dark brown in color and, to enhance details, it was coated with ammonium chloride before being photographed.

SYSTEMATIC PALEONTOLOGY

Order PELECANIFORMES Sharpe, 1891

Suborder SULAE Sharpe, 1891

Family PLOTOPTERIDAE Howard, 1969

Plotopterinae Brodkorb, 1971:174, as a subfamily of Phalacrocoracidae.

AMENDED DIAGNOSIS OF FAMILY.—The new taxon has an overall tarsometatarsal morphology closely resembling that of an unnamed plotopterid from Kyushu, Japan (Hasegawa et al. 1979). Although the published description of the Kyushu specimen is very brief and the figures are of an unprepared specimen, it appears to share with the new taxon the following combination of characters: tarsometatarsus with a high and rounded intercotylar prominence positioned off-center laterally; internal cotyla large, deeply concave, and open anterodistally; internal calcaneal ridge greatly enlarged and rounded proximally; shaft widened lateromedially and flattened anteroposteriorly; internal trochlea rounded and slightly knoblike anteriorly; middle trochlea longest, directed strongly anteriorly, positioned well off-center medially; external trochlea shortest, directed posteriorly; and large, deep metatarsal facet.

TYPE GENUS.—*Plotopterum* Howard, 1969.

INCLUDED GENERA.—*Plotopterum* Howard, 1969; *Tonsala* Olson, 1980; *Phocavis* new genus; unnamed genera from Japan.

Phocavis new genus

DIAGNOSIS OF GENUS.—Tarsometatarsus stout with slender and extremely anteroposteriorly flattened shaft; high and anterodistally overhanging intercotylar prominence; large, concave internal cotyla nearly twice as large as external cotyla; deep, medially placed metatarsal facet; middle trochlea longest, anteriorly directed, and off-center medially; external trochlea large and posteriorly directed; and internal trochlea large, posteriorly directed, and rounded anteriorly.

FIGURE 2. *Phocavis maritimus* new genus and species, holotype, right tarsometatarsus, LACM 123897, natural size. (*a*) Anterior; (*b*) medial; (*c*) posterior; (*d*) lateral; (*e*) proximal; (*f*) distal view.

ETYMOLOGY.—From Latin; *Phoca,* seal (the mammal), and *avis,* bird, in reference to the probable swimming habitus of the taxon.

TYPE SPECIES.—*Phocavis maritimus* new species.

Phocavis maritimus new species
(Figure 2)

DIAGNOSIS OF SPECIES.—As for the genus *Phocavis.*

ETYMOLOGY.—Latin; *maritimus,* seafaring, of the sea.

HOLOTYPE.—LACM 123897, right tarsometatarsus, lacking end of wing of internal trochlea, collected by the author, 28 October 1979.

TYPE LOCALITY.—LACM 5060. Rocks exposed along the north side of an abandoned railway roadbed at the west end of a cut near the center of the SE¼, SW¼, NE¼ of Section 8, T. 3N., R. 4W., Vernonia 7.5 minute quadrangle (1979 edition), Washington County, Oregon.

FORMATION AND AGE.—Upper part of the middle member of the Keasey Formation, Late Eocene. The Keasey Formation is exposed throughout the upper Nehalem River basin in northwestern Oregon and consists of approximately 700 m of tuffaceous siltstones and massive mudstones with locally abundant concretions. It has been subdivided into lower, middle, and upper members (Warren et al. 1945; Warren and Norbisrath 1946; Moore and Vokes 1953). The molluscan fauna from the Keasey Formation indicates a Late Eocene age (Hickman 1976, 1980, written comm. 1982) and deposition at depths of between 500 and 1,000 m (bathyal), although rare specimens of shallow water origin (apparently transported) have been found (Moore and Vokes 1953; Lindberg and Hickman 1986). The Keasey Formation is correlative with the *Echinophoria dalli* Molluscan Zone, Galvinian Molluscan Stage, Refugian Foraminiferal Stage, Priabonian Global Chronostratigraphic Stage, and the upper part of the Duchesnean Land Mammal Age of North America (Armentrout et al. 1983).

Other vertebrate fossils known from the Keasey Formation include a large bird, probably a pseudodontorn (currently under study), shark teeth (Welton 1972, 1973), teleost otoliths and bones, a marine turtle (University of California, Museum of Paleontology, Berkeley), and ceta-

cean vertebrae (Northwest Museum of Natural History, Portland State University, David Taylor, pers. comm.).

MEASUREMENTS (IN MM).—Length 59.6, width of proximal head 23.6, width of shaft at level of metatarsal facet 13.9, width of distal end through trochleae 25.7, width of middle trochlea 10.1.

DESCRIPTION.—The tarsometatarsus of *P. maritimus* differs from that of the unnamed plotopterid from Kyushu, Japan (Hasegawa et al. 1979) in being much smaller and more elongate (relative to proximal and distal width), and by having a hooklike and anterodistally overhanging intercotylar prominence; external cotyla more open anterodistally; hypotarsus with internal tendinal canal partially closed proximally; distal foramen separate from intertrochlear notch; internal trochlea extending farther distally; and external trochlea tilted more laterally.

Two measurements for the Kyushu tarsometatarsus are given by Hasegawa et al. (1979: 45): overall length (103.9 mm) and proximal (?) width (50.6 mm). The Kyushu specimen represents an animal approximately twice as large as *P. maritimus*. *Phocavis maritimus* was a much larger animal than *Plotopterum joaquinensis*, but may have been slightly smaller than *Tonsala hildegardae*. Newly discovered specimens of *T. hildegardae* from Washington are in preparation and under study and indicate that the tarsometatarsus, when found, may be more like that in *Anhinga* spp. than that of *P. maritimus*.

DISCUSSION

If the plotopterid specimens from Japan were not known, *Phocavis maritimus* would have been assigned to the Pelecaniformes, but could not have been assigned to any known family. There are, however, some superficial similarities between the tarsometatarsus of *P. maritimus* and living species in the pelecaniform family Anhingidae. The similarities between bones of the hindlimbs of the Plotopteridae and Anhingidae have been discussed by Olson and Hasegawa (1979, 1985) and Olson (1980, 1985), and further suggest the assignment of *P. maritimus* to the Plotopteridae.

Geologically, *P. maritimus* is much older than the described plotopterids from Japan and *Plotopterum joaquinensis* from California. Olson (1980) assigned an age of Late Oligocene to *Tonsala hildegardae*. The type locality for *T. hildegardae* is within Durham's (1944) *Echinophoria rex* (now *Liracassis rex*) molluscan zone, recently assigned an age of Early Oligocene (Moore 1984). A mollusk collection from rocks near the type locality for *T. hildegardae* (perhaps Durham's locality A3690), USGS M8986, contains *Liracassis apta* (Tegland 1931) and is Early Miocene in age (E. J. Moore, written comm. 1986). Durham (1944:110) assigned an age of Middle Oligocene to that part of his *Echinophoria* (*Liracassis*) *rex* molluscan zone. I think that *T. hildegardae* is older than Late Oligocene, but more work on the geology and biostratigraphy of the Pysht Formation must be done before *T. hildegardae* can be given a precise age assignment (see Domning et al. 1986:6–12).

It has been suggested that extinction of the Plotopteridae and, in the southern hemisphere, the giant penguins, was a result of the rise of seals and porpoises (Olson and Hasegawa 1979; Olson 1980, 1985), which presumably resulted in competition for the same food resources. Evidence now available, however, suggests that plotopterids and a previously unknown diversity of cetaceans, including small odontocetes, contemporaneously occupied the eastern North Pacific Ocean from at least as early as Late Eocene time until the apparent extinction of the Plotopteridae in Middle Miocene time. Cetacean vertebrae have been collected from the Keasey Formation and they are also known from Late Eocene and/or Early Oligocene age rocks on Vancouver Island (Kellogg 1936; Barnes 1977). Also, a variety of small, toothed cetaceans are known from Late Eocene and Oligocene age sediments of Washington (undescribed specimens, collections of U.S. National Museum, collections of LACM, and field observations). *Tonsala hildegardae* was found in the same rocks as a very diverse cetacean assemblage (Domning et al. 1986), which includes many different species of small archaic odontocetes.

A major change in marine endotherm faunas (Lipps and Mitchell 1976) occurs in latest Oligocene time with the appearance of the enaliarctine pinnipeds (Repenning and Tedford 1977; Barnes 1979). The rapid diversification and dispersal of these pinnipeds in the North Pacific Ocean in Late Oligocene and Early Miocene time may, in fact, be linked to the extinction of the Plotopteridae, but the extinction of the plotopterids and the nearly simultaneous appearance of the pinnipeds is more probably related to climatic events. Climate changes and the resultant

oceanographic changes which affect phytoplankton diversity can have enormous impact on marine vertebrate populations (Lipps and Mitchell 1976). Therefore, the global warming event that culminated at about 16.4 mya (Early Middle Miocene) and affected plankton and molluscan distributions may be a more probable cause for the extinction of the Plotopteridae (Orr and Faulhaber 1975; Barnes 1977).

Conclusions

A new genus and species of Late Eocene age bird, *Phocavis maritimus,* known only by a single tarsometatarsus, is the earliest known member of the Plotopteridae, an extinct family of the order Pelecaniformes. This is the third species of Plotopteridae known for North America and the first record of the family from Oregon. *Phocavis maritimus* was found in rocks of the upper part of the middle member of the Keasey Formation in northwestern Oregon, and was associated with a molluscan fauna that indicates a Late Eocene age and deposition at a depth of between 500 and 1,000 m. Therefore, unless the specimen is allochthonous, it may be inferred that the animal could move far off shore.

Because the only other described plotopterid tarsometatarsus is that from the partial skeleton of an unnamed taxon from Kyushu, Japan, *P. maritimus* cannot, at present, be directly compared to *Plotopterum joaquinensis* or *Tonsala hildegardae.* Differences in probable body size and geological age are, however, sufficient to further indicate that the Oregon fossil represents a new taxon.

Acknowledgments

I thank Lawrence G. Barnes, Kenneth E. Campbell, Jr., and Samuel A. McLeod, Natural History Museum of Los Angeles County; Ellen J. Moore, U.S. Geological Survey, Menlo Park; and Bruce J. Welton and Joann E. Welton, Chevron, for their support, suggestions, and reviews of this paper. I also thank Storrs L. Olson and David W. Steadman, who reviewed an early draft of this paper, and the various anonymous reviewers for their comments and suggestions. Carole S. Hickman, University of California, Berkeley, and David G. Taylor, Portland State University, provided biostratigraphic, geologic, and geographic information concerning the Keasey Formation in Oregon. The Natural History Museum of Los Angeles County provided technical support. Michael J. Stokes, LACM, advised me during final mechanical preparation of the specimen described here. Photographs of the specimen were done by John De Leon, LACM staff photographer. I especially thank my wife, Gail H. Goedert, for her assistance and support in the field.

Literature Cited

Armentrout, J. M., D. A. Hull, J. D. Beaulieu, and W. W. Rau. 1983. Correlation of Cenozoic stratigraphic units of western Oregon and Washington. Oregon Dep. Geol. and Min. Ind., Oil and Gas Inv. 7:1–90.

Barnes, L. G. 1977. Outline of eastern North Pacific cetacean assemblages. Syst. Zool. 25(4):321–343.

———. 1979. Fossil enaliarctine pinnipeds (Mammalia: Otariidae) from Pyramid Hill, Kern County, California. Contrib. Sci. Nat. Hist. Mus. Los Ang. Cty. 318:1–41.

Brodkorb, P. 1971. Catalogue of fossil birds: part 4 (Columbiformes through Piciformes). Bull. Fl. State Mus. Biol. Sci. 15(4):163–266.

Domning, D. P., C. E. Ray, and M. C. McKenna. 1986. Two new Oligocene Desmostylians and a discussion of Tethytherian systematics. Smithson. Contrib. Paleobiol. 59:1–56.

Durham, J. W. 1944. Megafaunal zones of northwestern Washington. Univ. Calif. Bull. Dep. Geol. Sci. 27:101–211.

Hasegawa, Y., S. Isotani, K. Nagai, S. Seki, T. Suzuki, H. Otsuka, M. Ota, and K. Ono. 1979. Preliminary notes on the Oligo-Miocene penguin-like birds of Japan. Kitakyushu Mus. Nat. Hist. Bull. 1:41–60.

Hasegawa, Y., Y. Okumura, and Y. Okazaki. 1977. A Miocene fossil bird from Mizunami, Central Japan. Bull. Mizunami Foss. Mus. 4:169–171.

Hickman, C. S. 1976. Bathyal gastropods of the family Turridae in the Early Oligocene Keasey Formation in Oregon, with a review of some deep-water genera in the Paleogene of the eastern Pacific. Bull. Amer. Paleo. 70(292):1–119.

———. 1980. Paleogene marine gastropods of the Keasey Formation in Oregon. Bull. Amer. Paleontol. 78(310):1–112.

Howard, H. 1929. The avifauna of the Emeryville Shellmound. Univ. Calif. Publ. Zool. 32(2):501–544.

———. 1969. A new avian fossil from Kern County, California. Condor 71(1):68–69.

Kellogg, A. R. 1936. A review of the Archaeoceti. Carnegie Inst. Wash. Publ. 482:1–366.

Lindberg, D. R. and C. S. Hickman. 1986. A new anomalous giant limpet from the Oregon Eocene (Mollusca: Patellida). J. Paleontol. 60(3):661–668.

Lipps, J. H. and E. Mitchell. 1976. Trophic model for the adaptive radiations and extinctions of pelagic marine mammals. Paleobiology 2(2):147–155.

Moore, E. J. 1984. Middle Tertiary molluscan zones of the Pacific Northwest. J. Paleontol. 58(3):718–737.

Moore, R. C. and H. F. Vokes. 1953. Lower Tertiary crinoids from northwestern Oregon. U.S. Geol. Surv. Prof. Paper 233-E:1–147.

Olson, S. L. 1980. A new genus of penguin-like pelecaniform bird from the Oligocene of Washington (Pelecaniformes:

Plotopteridae). Contrib. Sci. Nat. Hist. Mus. Los Ang. Cty. 330:51–57.

———. 1985. The fossil record of birds. Chapter 2 *in* Avian biology, Vol. 8. D. S. Farner, J. R. King, and K. C. Parkes, eds. Academic Press, Orlando, Florida.

Olson, S. L. and Y. Hasegawa. 1979. Fossil counterparts of giant penguins from the North Pacific. Science 206(4419): 688–689.

———. 1985. A femur of *Plotopterum* from the Early Middle Miocene of Japan (Pelecaniformes: Plotopteridae). Bull. Nat. Sci. Mus. (Tokyo), Ser. C, 11(3):137–140.

Orr, W. N. and J. Faulhaber. 1975. A middle Tertiary cetacean from Oregon. Northwest Sci. 49(3):174–181.

Repenning, C. A. and R. H. Tedford. 1977. Otarioid seals of the Neogene. U.S. Geol. Surv. Prof. Paper 992:1–93.

Sharpe, R. B. 1891. A review of recent attempts to classify birds. Comm. II Ornith. Congress, Budapest. 90 pp.

Tegland, N. M. 1931. Gastropod genus *Galeodea* in the Oligocene of Washington. Univ. Calif. Bull. Dep. Geol. Sci. 19:397–444.

Warren, W. C. and H. Norbisrath. 1946. Stratigraphy of the upper Nehalem River basin, northwest Oregon. Bull. Amer. Assoc. Petrol. Geol. 30(2):213–237.

Warren, W. C., H. Norbisrath, and R. M. Grivetti. 1945. Geology of northwestern Oregon, west of the Willamette River and north of latitude 45°15′. U.S. Geol. Surv. Oil and Gas Inv. Prel. Map 42, geol. map and text.

Welton, B. J. 1972. Fossil sharks in Oregon. Ore Bin 34(10): 161–170.

———. 1973. Oligocene selachians from the Keasey Formation at Mist, Oregon. Geol. Soc. Am., Abstr. with Prog. 5(1):121.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 7, pp. 103-110, 2 figs., 2 tables. February 5, 1988

A NEW SPECIES OF *ACANTHEMBLEMARIA* FROM MALPELO ISLAND, WITH A KEY TO THE PACIFIC MEMBERS OF THE GENUS (PISCES: CHAENOPSIDAE)

By

Richard H. Rosenblatt

Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093

and

John E. McCosker

Steinhart Aquarium, California Academy of Sciences, San Francisco, California 94118

ABSTRACT: A new chaenopsid blenny, *Acanthemblemaria stephensi* sp. nov., of the *hancocki* species complex is described from Isla Malpelo off the Pacific Coast of Colombia. *Acanthemblemaria stephensi* is distinguished from all its congeners by color pattern and details of head spination and is regarded as endemic to the oceanic Isla Malpelo. Vertebral numbers are given for all Pacific species of the genus, and an identification key is presented.

Submitted 16 April 1986. Accepted 27 February 1987.

INTRODUCTION

The family Chaenopsidae comprises a group of small, mostly tube-dwelling, blennioid fishes of the American tropics. The most speciose genus of the family is *Acanthemblemaria,* with 14 species currently recognized. The discovery of an additional species at the isolated volcanic Isla Malpelo, 345 km off the Pacific coast of Colombia, brings the total to 15, with 8 in the Atlantic and 7 in the Pacific. The last comprehensive review of the species of *Acanthemblemaria* was that of Stephens (1963), at which time four species were known from the Pacific. The addition of three species has created problems of identification. We therefore present a key to the Pacific species of the genus, and give data on vertebral numbers (Table 2).

Material of the new species was collected by a joint Smithsonian Tropical Research Institute/ U.S. Navy project, many results of which, including general descriptions of the geology and subtidal communities of Malpelo, have been published (Graham 1975).

METHODS AND MATERIALS

In general the methods of Stephens (1963) have been followed except that the parietals of Stephens are frontals in our terminology and procurrent caudal rays were not enumerated.

Head pore terminology is mostly that of Smith-

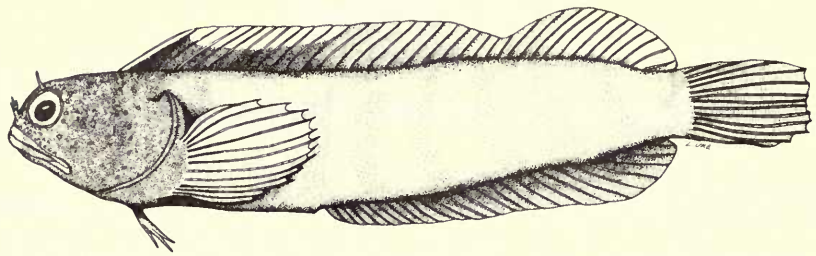


FIGURE 1. *Acanthemblemaria stephensi* Rosenblatt and McCosker, sp. nov. Illustration of the holotype, SIO 72-79, a 33.1 mm (SL) male.

Vaniz and Palacio (1974). Johnson and Greenfield (1976) modified that terminology by introducing the name "commissural pore(s)" for median pores in the frontals, "anterofrontal pores" for the pores at the anterior termination of each frontal, and "nasal pores" for the pores at the anterior end of the nasals. Although pore terminology would seem to be sufficiently encumbered now, it is advantageous to recognize yet another pore group in *Acanthemblemaria.* This may be termed the median interorbital group. It consists of one to six pores on the frontals in or on the edge of the interorbital groove (see Fig. 2E). There are always one or two median pores (commissural pores of Johnson and Greenfield) and from zero to four lateral pores, depending on the species. The lateral pores are posterior to the median pore(s). The lateral pores were included in the count of frontal pores by Stephens (1963) with Smith-Vaniz and Palacio (1974). The latter authors did not include median pores in their extensive discussion other than to state that "interorbital pores were not included in the frontal pore count." However, they did illustrate them in figures 4, 5, and 6. Stephens referred to median pores, but did not illustrate them, and it is difficult to interpret his counts.

As proportional measurements are almost never used in the identification of these fishes, and because most of our type material is distorted and not well preserved, measurements are presented only for the holotype. Vertebral and dorsal and anal ray counts were made from radiographs. There is considerable variability in which vertebra bears the first haemal spine; the vertebra with which the pterygiophores of the anal spines are associated was always counted as the first caudal vertebra. Counts include the ural centrum.

Specimens utilized are housed in the Ichthyology Department, California Academy of Sciences (CAS), or the Marine Vertebrates Collection, Scripps Institution of Oceanography (SIO). Material utilized in preparation of Table 2 is as follows: *A. balanorum,* SIO 62-55; *A. castroi,* CAS 36989, CAS 36990, CAS 39246, CAS 39254, CAS 39333, SIO 69-1003; *A. crockeri,* CAS uncat. Acc. 1964-VII, CAS W51-8, CAS W52-51; *A. exilispinus,* CAS 35574, CAS 35643; *A. hancocki,* CAS 34473, SIO 70-359; and *A. macrospilus,* SIO 65-318.

Acanthemblemaria stephensi
Rosenblatt and McCosker, sp. nov.
(Figures 1, 2A, B)

Acanthemblemaria new species. McCosker and Rosenblatt 1975: 93. Listed.

DIAGNOSIS.—An *Acanthemblemaria* with posterior frontal spines small and erect, in a triangular patch crossing midline of head, with posterior margin of patch curved and extending behind orbits less than one-half way to dorsal origin. Orbital flange of second infraorbital smooth. Orbital tentacle simple. Body plain brown or with indistinct bars; head of males dark,

→

FIGURE 2. Scanning electron micrographs of the cranial spines and pore patterns of the Pacific species of *Acanthemblemaria.* All specimens are males. The location of the median interorbital pores are indicated by arrows on E. (A, B) *A. stephensi,* SIO 72-97, 36 mm (SL), paratype; (C) *A. macrospilus,* SIO 65-318, 37 mm (SL); (D) *A. hancocki,* CAS 35644, 29 mm (SL); (E) *A. balanorum,* SIO 62-55, 35 mm (SL); (F) *A. castroi,* CAS 30912, 35 mm (SL); (G) *A. exilispinus,* CAS 35643, 39 mm (SL); and (H) *A. crockeri* CAS 58051, 33 mm (SL).

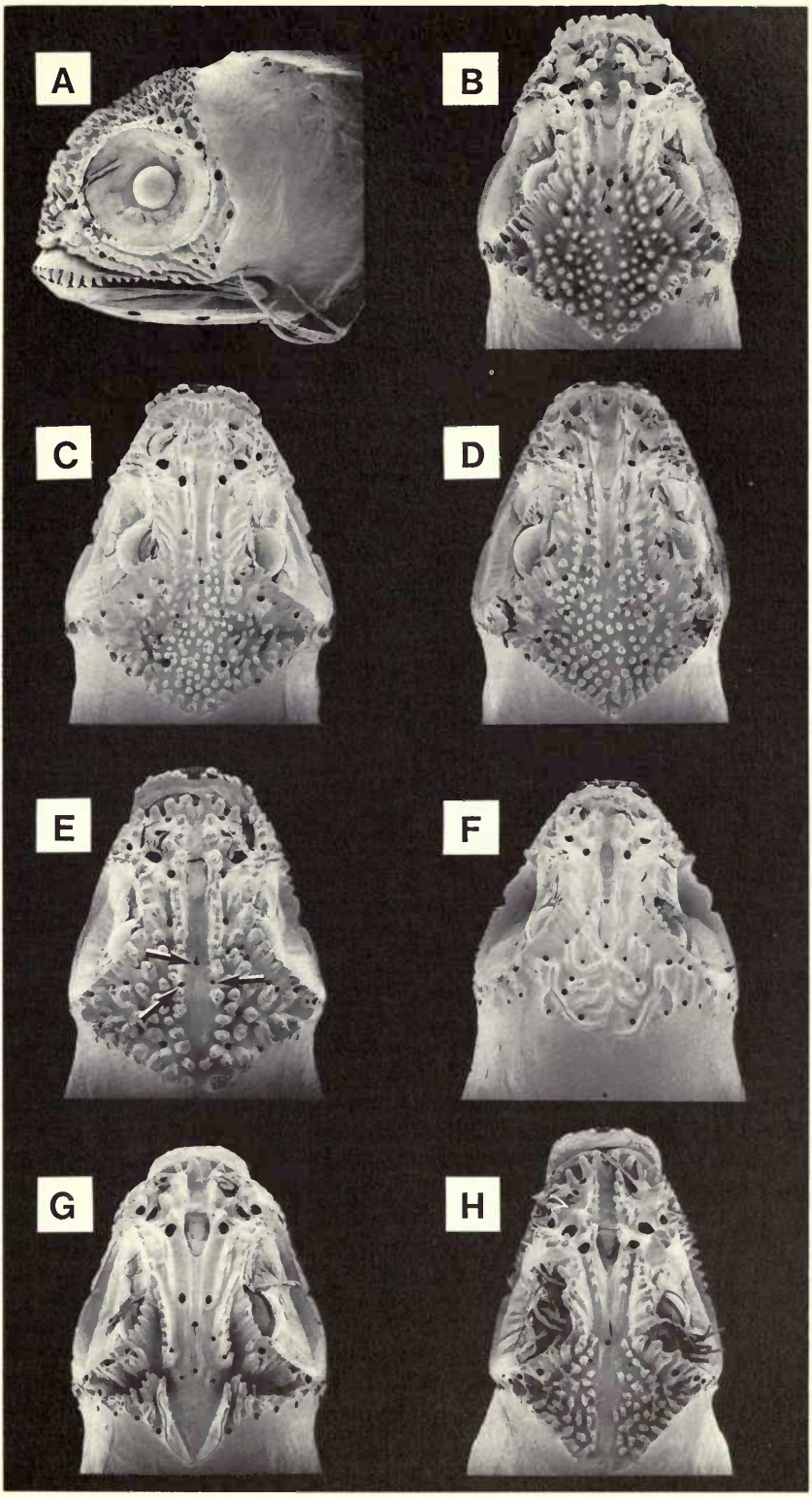

A
B
C
D
E
F
G
H

TABLE 1. FREQUENCY DISTRIBUTION OF DORSAL RAYS IN *ACANTHEMBLEMARIA STEPHENSI*. Asterisk indicates count of holotype.

Soft rays	Spines			
	22	23	24	25
11				1
12	1	7	21*	
13			1	

and strongly contrasted with body. The new species may be separated from its closest relatives using the characters within the key.

MEASUREMENTS OF HOLOTYPE (IN MM).—Standard length 33.1; head length 8.5; head depth 5.0; upper jaw length 5.0; orbit length 2.1; snout length 1.4; interorbital width 1.6; predorsal length 5.5; preanal length 15.2; caudal peduncle length 2.5; pectoral length 5.2; longest dorsal spine 6.9; orbital cirrus length 1.0.

DESCRIPTION.—(Additional meristic data are in Tables 1 and 2.) Values in parentheses are means ± one standard error. Total dorsal rays 34–37 (35.7 ± 0.10); dorsal spines 22–25 (23.8 ± 0.15); dorsal soft-rays 11–13 (12.0 ± 0.18); anal rays II, 24–25 (24.1 ± 0.05); pectoral rays 13.0 (n = 42); vertebrae 41–43 (41.8 ± 0.09); pelvic rays I,3; principal caudal rays 13.

Body relatively elongate, as in all chaenopsids. On a continuum within the genus *Acanthemblemaria* from slender and elongate in *A. chaplini* through intermediate in *A. exilispinus* to robust in *A. castroi, A. stephensi* falls between the two latter species. Head length 3.7–4.0 in standard length. Depth of head about 1.5 and width about 1.8 in head length. Upper jaw about 2 in head, extending about to posterior margin of 2nd infraorbital. Orbit about 2 in upper jaw length. A simple, slender orbital tentacle on dorsal margin of eye. Tentacle in males slightly longer than pupil length, that of females about one-half as long. Anterior nostril in a short tube surmounted by a palmately-branched posterior flap. Opercle free from body dorsally.

An outer row of 10–12 teeth on each premaxilla. Medial teeth flattened, protruding, and almost incisiform, lateral teeth decreasing in size and becoming progressively more pointed. An inner patch of small teeth, pointed in females and almost granular in males, behind medial teeth. Lower jaw with a row of 8 incisiform teeth on expanded anterior portion and about 10 stout conical teeth on straight portion. A patch of small teeth behind incisors. Vomer with 2 stout teeth, one behind the other, on each side. Palatines with two rows of stout teeth, 7 in outer row and 4 in inner.

Head spines are illustrated in Figure 2. Two rows of blunt spines on first infraorbital, one on ventral margin, and another at mid-width. Upper margin with one or two anterior spines, otherwise smooth. Second infraorbital with a few rugosities ventrally on surface, margins smooth. Nasals with a semicircle of spines medial to, and a patch of spines lateral to, anterior nostril. An isolated spine at the level of and medial to each posterior nostril. Frontal bones spinose. A row of spines on orbital rim, extending from articulation with nasal to about level of pupil posteriorly. A weak notch where anterior and posterior orbital flanges meet, at level of orbital tentacle. Two rows of spines on each side between orbits, separated by a median groove. Posterior to rear margin of pupil the interorbital rows broaden into a broadly triangular to rounded patch of spines that is continuous across the top of the head. The posterior margin of this

TABLE 2. FREQUENCY DISTRIBUTION OF VERTEBRAL NUMBER IN PACIFIC SPECIES OF *ACANTHEMBLEMARIA*. Asterisk indicates count of holotype.

	Precaudal				Caudal							Total						
	10	11	12	13	29	30	31	32	33	34	35	41	42	43	44	45	46	47
balanorum		17					4	9	3	1			4	9	3	1		
castroi		13						4	6	2	1			4	6	2	1	
crockeri		8	17					9	12	3	1				13	7	3	1
exilispinus			10	2	1	10	1					1	8	3				
hancocki	2	23				8	15	2				8	15	2				
macrospilus		11						8	3					8	3			
stephensi		31*				8	22*	1				8	22*	1				

patch slightly behind the rear margin of the orbits. Spines more pointed, and slightly larger, in males.

Mandibular pores 4; common pores (between mandibular and preopercular series) 2, one above the other, the ventral smaller; preopercular 5; lateral supratemporal 5; median supratemporal 3, arranged in a forward-directed triangle; supraorbital 3 or (usually) 4; posterior infraorbital 5; anterior infraorbital 2; frontal 6; median interorbital 3; anterior frontal 1; nasal 2.

Dorsal origin just behind occiput, over preopercle. Spinous dorsal low, spines increasing gradually in length to about the 20th, then decreasing to last. First dorsal soft-ray abruptly higher, so that fin is notched. Margin of soft dorsal rounded. Last dorsal and anal rays attached to caudal peduncle by a membrane well before insertion of first principal caudal ray. Anal fin relatively low, its margin straight anteriorly, rounded posteriorly. Caudal margin truncate to rounded. Pectorals fanlike, the lower three or four rays somewhat thickened and exserted, more in males. Middle pelvic soft-ray longest, fin membrane not extending to tips of pelvic rays.

Color descriptions are based on alcoholic specimens. Body ground color of males evenly brown or dark tan, with a suggestion of barring. Head dark, almost black, particularly ventral parts and branchiostegal membrane, so that it contrasts strongly with the body. Lips white medially about as far back as level of the pupil, as is the underside of chin. Nasal and orbital tentacles white. (It is likely that the white areas are red in life, as is the case in *Coralliozetus angelica*.) Spinous dorsal with a darker area between 1st and 2nd spines, remainder of fin dusky basally, clear distally on its anterior part, entire fin becoming dusky posteriorly. Anal dusky, darker near margin, so that when fin is depressed there is the appearance of a dark edging. Pectorals and caudal rays dusky, membranes clear. Lower 4–6 pectoral rays of males white distally. Pelvics dusky.

Females differ chiefly from males in that the body and head are lighter and more uniform in color, so that the head is not as contrasted with the body. Also, there is a dark area of pigment on the head that rims the lower margin of the orbit and then runs across the chin just behind the mandibular symphysis. In general the fins are lighter and less contrastingly colored in females. A female from SIO 72-97 has a unique body color pattern. There is a row of 7 dark spots along the midline beginning under the middle of the spinous dorsal. The first 5 spots have lighter centers. There are also 7 small dots along the dorsal base, over the interspaces between the spots. The closest approach to this color pattern among the other females is found on a few individuals that have 5 or 6 vague broad bars.

MATERIAL EXAMINED.—All specimens were collected between 29 February and 3 March 1972 by personnel of the Smithsonian party (Graham 1975). Holotype: SIO 72-79, a 33.1 mm male taken with rotenone on the NE side of Isla Malpelo, Colombia (3°51′07″N, 81°35′40″W), at a depth of 0–10 m on 3 March 1972, by Jeffrey B. Graham and party. Paratypes: SIO 72-97, taken with and bearing the same data as the holotype, 38 (17–33 mm); SIO 72-96, Isla Malpelo, 17 (16–40 mm); CAS 31542, Isla Malpelo, 4 (29–37 mm).

ETYMOLOGY.—Named for John S. Stephens, Jr., the major contributor to present knowledge of systematics of the Chaenopsidae.

DISTRIBUTION.—Known only from Isla Malpelo, Colombia. It may be that *A. stephensi* also occurs on the mainland, but remains uncollected there. This is of course possible, considering that the area south of Panamá has not been collected very systematically or intensively. However the Argosy Expedition did include rotenone stations in Colombia and Ecuador (Stephens et al. 1966) and did not find this species, although other chaenopsids were taken. Also, on biogeographic grounds, a species living on the Colombian coast would be expected to occur as far north as Panamá and Costa Rica (Stephens 1963), areas that have been well collected by ichthyocide and diving. McCosker and Rosenblatt (1975) noted certain elements in the fish faunas linking Malpelo and the Galápagos Islands and *A. stephensi* might be expected to occur at that group. However, it is unlikely that *A. stephensi* occurs undiscovered at the well-collected Galápagos. If *A. stephensi* is indeed a Malpelo endemic, it is not unique. Three other fishes, two alpheid shrimps, a crab, and a starfish are thus far known only from the island (papers *in* Graham 1975). Malpelo is a small island (about 2 × 0.75 km) with a perimeter of approximately 6 km. All of the endemic species belong to groups with larvae that are, at least for a time, planktonic. Nothing is known of detailed current patterns around the island, but conservation of young must be a major problem faced by the Malpelo endemics.

GENERIC PLACEMENT.—According to Stephens

(1963) two morphological features unite the species placed in *Acanthemblemaria* and separate them from all other chaenopsids. These are the presence of spines on the frontal bones and the arrangement of the palatine teeth in 2 rows. However, Stephens and Cervigon (*in* Stephens 1970) subsequently described a species of *Emblemaria, E. diphyodontis,* with biserial palatine teeth, which consequently will not run to a genus in Stephens's (1963) key. The independent acquisition of this feature by a single species of *Emblemaria* does not necessarily vitiate it as an indicator of relationship of the species of *Acanthemblemaria.* The high spinous dorsal, lack of head spines, and other characters indicate that *E. diphyodontis* is properly placed in *Emblemaria,* and that the presence of 2 rows of palatine teeth in *Acanthemblemaria* and *E. diphyodontis* is a homoplasy.

Another aspect of jaw structure and dentition is worthy of comment. The lower jaw in *Acanthemblemaria* is expanded distally, then abruptly constricted, with the rami straight and almost parallel. This formation has been variously described as resembling an old-fashioned keyhole (Beebe and Tee-Van 1938) or the jaws of a hippopotamus (Myers and Reid 1936), and illustrated by Böhlke (1957). The peculiar shape has a functional significance. The incisiform teeth on the expanded anterior portion of the lower jaw oppose similar teeth on the premaxillae. However the stout teeth on the rami of the lower jaw oppose the equally stout palatine teeth, providing a sort of "double-grip."

The species currently placed in *Acanthemblemaria* do seem to form a natural group. That is, taken pairwise and severally they are more similar to one another than to other chaenopsids, although the only unequivocal specialization is the presence of serrations or spines on the supraorbital ridge of the frontals, and even these may be much reduced in *A. castroi.*

IDENTIFICATION.—The characters given in the diagnosis serve to distinguish *A. stephensi* from its congeners. The number of Pacific species of *Acanthemblemaria* has almost doubled since Stephens's (1963) treatment. Therefore a key to the Pacific species is presented here:

1A. Orbital tentacle bushlike, with several branches springing from a common base; a dorsoventrally oval, chocolate-brown spot, outlined with black, on cheek, covering area between orbit and opercle ..... *A. crockeri* Beebe and Tee-Van, 1938. Gulf of California

1B. Orbital tentacle not bushlike, simple, bifid near tip or pinnately branched; no such spot on cheeks (a dorsal dark area, if present, to midline only) 2

2A. Posterior frontal spines in 2 isolated patches borne on elevated ridges, each patch smaller than eye diameter in maximum dimension (Fig. 2G); 5 vomerine teeth in a crescentic row; precaudal vertebrae 12–13 ..... *A. exilispinus* Stephens, 1963. Port Parker, Costa Rica to Isla de la Plata, Ecuador

2B. Posterior frontal spines continuous across midline of head or separated by a narrow groove into 2 patches each larger than a pupil diameter, or represented by low ridges (Fig. 2A–F); vomerine teeth 4, 2 on each side of vomer; precaudal vertebrae 10 or 11 3

3A. Head spines high and conspicuous, often club-shaped; frontal spines separated by a groove which may almost be roofed by expanded tips of spines (Fig. 2E); caudal emarginate ..... *A. balanorum* Brock, 1940. Gulf of California to Bahía de Banderas, México

3B. Head spines blunt to pointed, or represented by low ridges; posterior frontal spines either continuous across midline or separated only anteriorly by a backward prolongation of interorbital groove (Fig. 2A, C, D, F); caudal rounded to truncate 4

4A. Posterior prolongation of infraorbitals at lower rear corner of eye long, reaching back to rictus, and covering entire maxilla; frontal spines either sparse, low, and blunt, or represented by low ridges[1] (Fig. 2F); head of males not dark and sharply

[1] The presence of spines or ridges on the frontals is not a simple function of size of specimen as suggested by Stephens and Hobson (*in* Stephens et al. 1966). Our largest specimen (a 52.5 mm male paratype, SIO 64-1003) has discrete spines, but two females from the same lot, 24 and 28 mm, respectively, have skin-covered ridges. Although all of the specimens with ridges and spines are males, females rarely may have serrated ridges, and a 40 mm male has ridges only.

contrasted with body color ..... *A. castroi* Stephens and Hobson, *in* Stephens et al. 1966. Galápagos Islands

4B. Junction of infraorbitals at lower rear corner of eye rounded to acute, never prolonged as above; frontal spines numerous and pointed (Fig. 2A, C, D); head of males dark and sharply contrasted with body color 5

5A. Orbital flange of second infraorbital smooth (Fig. 2B); body plain brown or lightly barred ..... *A. stephensi* sp. nov. Isla Malpelo, Colombia

5B. Rim of orbital flange of second infraorbital serrate, or with tubercles; a series of spots down sides 6

6A. A single row of 6 to 8 large brown spots, most larger than orbit diameter, along sides; dorsal spines 23–25, usually 24, anal soft-rays 24–26, usually 25 ..... *A. macrospilus* Brock, 1940. Gulf of California to Acapulco; Islas Revillagigedo, Isla del Coco, Costa Rica

6B. Three rows of small brown dots along sides; dorsal spines 23–24, usually 23, anal soft-rays 23–25, usually 24 ..... *A. hancocki* Myers and Reid, 1936. Port Parker, Costa Rica to Isla de la Plata, Ecuador

RELATIONSHIPS.—The morphological similarity of the Pacific species *A. hancocki, macrospilus,* and *balanorum* was noted by Stephens (1963), who referred to them as the "*hancocki* species group." Stephens et al. (1966) placed *A. castroi* in the group, and subsequently Smith-Vaniz and Palacio (1974) referred *A. rivasi* Stephens, 1970, of the Atlantic to the group. Stephens had related the three Pacific species mainly on the basis of having blunt head spines not arranged in isolated patches. Smith-Vaniz and Palacio further characterized the group as having "rather robust bodies, typically 10 or 11 precaudal vertebrae, dorsal fin distinctly notched at junction of spinous and segmented rays, supraorbital cirrus usually simple or bifid and vomerine teeth separated by a median hiatus." We agree both with the reality of the *hancocki* group and its species composition, although none of the defining characters, with the exception of the median toothless space on the vomer, can be demonstrated to be a synapomorphy. There is variability within the *hancocki* group in the arrangement of the pores of the median interorbital group. All the species except for *A. balanorum* and *castroi* have two median pores and no posterior lateral ones (e.g., Fig. 2B). *Acanthemblemaria castroi* is unique in the genus in having 2 pairs of posterior laterals (Fig. 2F). *Acanthemblemaria balanorum* (Fig. 2E) agrees with the Atlantic species *chaplini, medusa, greenfieldi, betinensis,* and *maria* and the Pacific *crockeri* in having a triangle of a single median and 2 posterior lateral pores. This latter arrangement is also found in *Ekemblemaria,* regarded by Stephens (1963) as the plesiomorphic sister group of *Acanthemblemaria.*

Acanthemblemaria balanorum then is the plesiomorphic sister group of the other *hancocki* group species. *Acanthemblemaria castroi* has retained the lateral pores and is autapomorphic in the presence of another pair of posterior lateral pores and the coalescence of head spines into ridges. It is the plesiomorphic sister group of *A. hancocki, macrospilus, rivasi,* and *stephensi,* which are synapomorphic in loss of the posterior lateral pores.

Acanthemblemaria stephensi is most similar to *A. hancocki.* In particular, the two agree in details of spination of the frontals, in that the frontal spines are short and numerous and the interorbital groove does not continue posteriorly so as to separate the frontal spines into two patches behind the eye. In this feature the two species agree with *A. rivasi* of the Atlantic, which also is similar in having a black spot or streak between the first and second dorsal spines. (This last feature is also found in some male specimens of *A. castroi,* and other species in the genus have dark areas on the anterior part of the dorsal, although not in that precise place.) *Acanthemblemaria hancocki* and *rivasi* further agree, and differ from *A. stephensi,* in having a series of spots along the midline, and saddles along the base of the dorsal. *Acanthemblemaria macrospilus* also has this coloration. *Acanthemblemaria hancocki* and *macrospilus* agree, and differ from *rivasi* and *stephensi,* in having spines on the flange of the posterior infraorbital. Such spines are present in the Atlantic *A. maria* and *spinosa* as well, but this may reasonably be regarded as a homoplasy, since these species represent the extreme of spine development in the genus. *Acanthemblemaria rivasi* and *A. castroi* are unique in the genus in having a rear prolongation

of the infraorbitals at their juncture. The species have little else in common beside generic characters, and it is unlikely that this feature, which functionally improves lateral bracing of the upper jaw (Rosenblatt and Stephens 1978) indicates any particularly close relationship.

Smith-Vaniz and Palacio (1974) have commented on the difficulty of constructing a phylogeny for the species of *Acanthemblemaria.* Although we have been able to further clarify relationships within the *hancocki* group, we can still only concur. It may be that in this and other speciose genera of reef fishes, a real understanding of relationships and phylogeny awaits the application of nonmorphological techniques such as biochemical genetics.

Acknowledgments

Much of the work on this paper was done during the senior author's sabbatical leave as a Research Associate at the California Academy of Sciences. H. J. Walker and Ms. Darcy Gibson furnished information and specimens from the Scripps Institution collection. Jeffrey Graham, then of the Smithsonian Tropical Research Institute, supplied the type material of *A. stephensi* to us for study. The illustration of the holotype was drawn by Lisa Katter-Uwe. Radiographs were prepared by M. Eric Anderson, and SEM pictures by Mary Ann Tenorio, CAS. Christina Slager provided valuable translation service.

Literature Cited

Beebe, W. and J. Tee-Van. 1928. The fishes of Port-au-Prince Bay, Haiti. Zoologica (N.Y.) 10(1):1–279.

———. 1938. Eastern Pacific expeditions of the New York Zoological Society. 15: Seven new fishes from Lower California. Zoologica (N.Y.) 23:299–312.

Bohlke, J. E. 1957. The Bahaman species of emblemariid blennies. Proc. Acad. Nat. Sci. Phila. 109:25–57.

Brock, V. E. 1940. Three new blennioid fishes from the west coast of Mexico. Stanford Ichthyol. Bull. 2:29–35.

Graham, J. B., ed. 1975. The biological investigation of Malpelo Island, Colombia. Smithson. Contrib. Zool. 176:1–98.

Johnson, R. K. and D. W. Greenfield. 1976. A new chaenopsid fish, *Emblemaria hyltoni,* from Isla Roatan, Honduras. Fieldiana Zool. 70(2):13–27.

McCosker, J. E. and R. H. Rosenblatt. 1975. Fishes collected at Malpelo Island. Smithson. Contrib. Zool. 176:91–93.

Myers, G. S. and E. D. Reid. 1936. Description of a new blennioid fish of the genus *Acanthemblemaria* from the Pacific coast of Panamá. Univ. South. Calif., Hancock Pac. Exp. 2(3):7–10.

Rosenblatt, R. H. and J. S. Stephens, Jr. 1978. *Mccoskerichthys sandae,* a new and unusual chaenopsid blenny from the Pacific coast of Panamá and Costa Rica. Contrib. Sci. Nat. Hist. Mus. Los Ang. Cty. 293:1–22.

Smith-Vaniz, W. F. and F. J. Palacio. 1974. Atlantic fishes of the genus *Acanthemblemaria,* with description of three new species and comments on Pacific species (Clinidae: Chaenopsinae). Proc. Acad. Nat. Sci. Phila. 125(11):197–224.

Stephens, J. S., Jr. 1963. A revised classification of the blennioid fishes of the American family Chaenopsidae. Univ. Calif. Publ. Zool. 68:1–133, 15 pls.

———. 1970. Seven new chaenopsid blennies from the western Atlantic. Copeia 1970(2):280–309.

Stephens, J. S., Jr., E. S. Hobson, and R. K. Johnson. 1966. Notes on distribution, behavior, and morphological variation in some chaenopsid fishes from the tropical eastern Pacific with descriptions of two new species, *Acanthemblemaria castroi* and *Coralliozetus springeri.* Copeia 1966(3): 424–438.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 8, pp. 111-132, 8 figs., 1 table February 5, 1988

A SYSTEMATIC STUDY OF *BRAVAISIA* DC. (ACANTHACEAE)

By

Thomas F. Daniel

Department of Botany, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

ABSTRACT: A taxonomic treatment of the neotropical genus *Bravaisia* is presented in which three species are recognized: *B. berlandieriana, B. grandiflora,* and *B. integerrima.* The genus belongs to the Trichanthereae where it is allied morphologically with *Trichanthera.* A key to the genera of Trichanthereae is provided. *Bravaisia* is distributed from Mexico and Cuba southward to northern South America, with all three species occurring in southeastern Mexico and northern Central America. Based on an estimate of phylogenetic branching patterns using *Trichanthera* as an outgroup, *B. integerrima* appears to be the sister group of *B. grandiflora* and *B. berlandieriana.* Honey bees are the predominant visitors to flowers of *B. integerrima* in Mexico.

Submitted May 27, 1987. Accepted August 7, 1987.

INTRODUCTION

Bravaisia DC. is a small genus of the predominantly tropical family Acanthaceae. This is the first attempt in this century to delimit all species in the genus. Of the 10 species that have been described in *Bravaisia* and in genera now recognized as congeneric with it, 3 are recognized here. These occur from northeastern Mexico and Cuba southward to Colombia and Venezuela.

Bravaisia is unusual among Mexican and Central American Acanthaceae in that at least two species are commonly mangrove trees. Mangrove plants or mangroves (as distinguished from mangrove communities or mangals) can be defined as tropical or subtropical ligneous plants that occur in intertidal and adjacent communities (modified from Tomlinson 1986). Such plants exhibit various adaptations (e.g., aerial roots in many) to their environment. Although certain other Acanthaceae attain tree size (e.g., species of *Ruellia* L., *Trichanthera* Humb. and Bonpl., and *Louteridium* S. Watson) or exhibit a mangrove habit (e.g., species of *Acanthus* L. in the Old World) mangrove trees are not currently known among other Latin American genera of the family. *Trichanthera gigantea* (Humb. and Bonpl.) Nees, a medium-sized tree that commonly occurs along streams and in swampy regions in northern South America and southern Central America, often has prop roots. It may eventually be shown to occur as a mangrove as well.

The following study provides a taxonomic revision of the genus and offers information on possible phylogenetic relationships and reproductive biology.

MATERIALS AND METHODS

This study is based on information obtained from more than 650 herbarium specimens and

field work in Mexico during 1982 and 1987. The citations of herbaria in the text follow abbreviations of Holmgren et al. (1981). All measurements were made on dried material. Pollen was measured using a compound microscope and a calibrated ocular micrometer. The grains were mounted in Diaphane prior to observation and measurement. Surface features were observed on untreated pollen with a scanning electron microscope. Pollen stainability was determined using analine blue in lactophenol. Pollination of stigmas was determined using a hand lens (10×).

Taxonomic History

The first species described in this genus was attributed to the Verbenaceae as *Amasonia integerrima* (Sprengel 1825). Lacking fruiting material, A. P. de Candolle (1838, 1845) treated his new genus *Bravaisia,* with its sole species, *B. floribunda,* as belonging to the Bignoniaceae. In June of 1847, Lemaire correctly attributed a nonfruiting collection of this genus, which he described as *Androcentrum multiflorum,* to the Acanthaceae. Later that same year, Nees (1847) attributed the two species of this genus described by him, *Onychacanthus cumingii* and *O. berlandierianus,* to the Acanthaceae as well. He did not see material of Lemaire's genus and was therefore unable to compare it to his own genus *Onychacanthus.* In the additions and corrections published with volume 11 of the Prodromus, Nees added a treatment of *Androcentrum.* Based on Lemaire's description, however, Nees was able to place it in tribe Ruellieae near *Onychacanthus.* Subsequently Oersted (1854) described *O. speciosus,* and Karsten (1865) described *O. arboreus.* Bentham (1876) was first to treat *Bravaisia* in the Acanthaceae and to recognize that it is identical to *Onychacanthus.* He did not make new combinations for the various species, however. Additional species of *Bravaisia* were described by Hemsley in 1886 (*B. tubiflora*), Smith in 1902 (*B. grandiflora*), and Blake in 1917 (*B. proxima*). Standley (1926) noted that Sprengel's *Amasonia integerrima* was conspecific with de Candolle's *Bravaisia floribunda.* He included *O. berlandierianus* in the synonymy of this species and suggested that *Androcentrum multiflorum* should likely be considered conspecific here as well. Leonard (1951) included all of the species described in *Onychacanthus* in the synonymy of *B. integerrima.* Gibson (1974) considered *B. proxima* to be conspecific with *B. grandiflora.*

Infrafamilial Relationships

Nees (1847) treated species of *Bravaisia* (as *Onychacanthus*) in his tribe Ruellieae, where they were aligned with *Trichanthera, Macrostegia* Nees, *Sclerocalyx* Nees (=*Ruellia* sp.), *Ophthalmacanthus* Nees (=*Ruellia* spp.), *Whitefieldia* Hook., *Ancylogyne* Nees (=*Sanchezia* Ruiz and Pavón), and *Androcentrum* Lemaire (=*Bravaisia*). After removing *Ophthalmacanthus* and *Whitefieldia,* Bentham (1876) treated this assemblage as tribe Ruellieae subtribe Trichanthereae. The wholly American subtribe was distinguished from other subtribes of Ruellieae by the combination of its *Ruellia*-like corollas; equidistant or subconnate (in pairs) filaments; herbaceous or subcoriaceous, obtuse (except in a few species of *Sanchezia*) calyx lobes; and trichotomously cymose-corymbose, capitate, or rarely spicate inflorescences that are borne at the apices of branches (or sometimes the inflorescence of axillary cymes). These same six genera (the name *Sclerocalyx* was replaced by the earlier name *Gymnacanthus* Nees) were considered by Lindau (1895) as tribe Trichanthereae of his subfamily Acanthoideae. The tribe was distinguished by "Rippenpollen," five-parted calyces, and firm, equally five-parted corollas with contorted lobes. With the exclusion of *Macrostegia,* which was shown to belong to the Verbenaceae (Macbride 1934), Lindau's Trichanthereae were accepted as a tribe of the subfamily Ruellioideae by Bremekamp (1965). He noted that the Trichanthereae differed from other Acanthaceae by their large size and by their pollen. He further noted the following attributes of the tribe: terminal paniculiform or racemiform inflorescences; obtuse calyx lobes; fleshy, actinomorphic corollas with the lobes contorted in bud; and glabrous seeds.

Of the six genera treated by Lindau (1895) in the Trichanthereae, three (*Bravaisia, Sanchezia,* and *Trichanthera*) are currently recognized. Two additional genera, *Trichosanchezia* Mildbr. and *Suessenguthia* Merxm., that would be included in this tribe because of their relationship to *Sanchezia* have been described in this century. *Sanchezia* (including the monotypic *Steirosanchezia* Lindau that was described in 1904) comprises 59 species concentrated in the wet forests of

northwestern South America (Leonard and Smith 1964). *Suessenguthia* consists of four species restricted to Peru and Bolivia (Wasshausen 1970). *Trichosanchezia* is a monotypic genus of Peru (Leonard and Smith 1964). *Trichanthera* consists of two species restricted in distribution to northern South America and southern Central America (Costa Rica and Panama).

Phylogenetic ancestors of the Trichanthereae were likely some part of the typical, four-stamened Ruellioid lineage with corolla lobes contorted in bud. The Trichanthereae differ most conspicuously from this assemblage, which includes *Ruellia,* in features of their pollen (summarized in Raj 1961, although descriptions of pollen have not been reported from either *Suessenguthia* or *Trichosanchezia*). The large size of some Trichanthereae, noted by Bremekamp (1965), is not unique to this tribe. Certain species of *Ruellia* (tribe Ruellieae) and *Louteridium* (tribe Louteridieae) in the Ruellioideae also attain the stature of moderate-size trees.

Despite the relatively large number of species described in *Sanchezia,* the genus remains poorly known. For example, fruits are unknown for most of the species. Likewise, fruits have yet to be described for *Suessenguthia* and *Trichosanchezia.* Therefore a thorough phylogenetic assessment of this tribe will not be possible until *Sanchezia* and its relatives become better known.

Based on data available in Leonard and Smith (1964), information provided by Dieter C. Wasshausen of the Smithsonian Institution (in litt.), and my studies of *Bravaisia* and *Trichanthera* the following key serves to distinguish genera of the Trichanthereae.

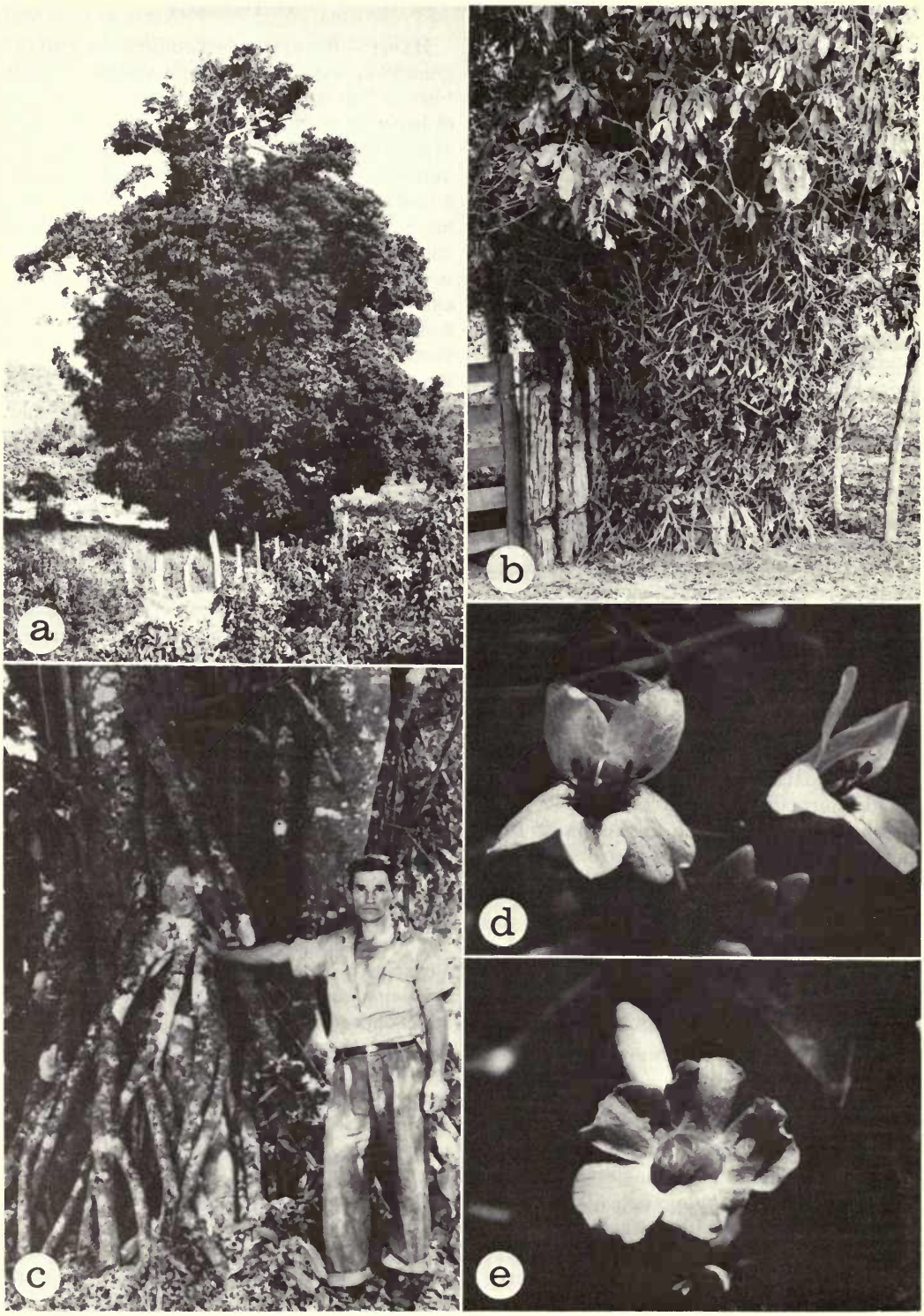
1. Corolla subcylindric; fertile stamens 2 or 4.
   2. Fertile stamens 2 ..... *Sanchezia*
   2. Fertile stamens 4.
      3. Thecae awned at base ..... *Suessenguthia*
      3. Thecae awnless ..... *Trichosanchezia*
1. Corolla campanulate; fertile stamens 4.
   4. Thecae awnless, rounded at base; capsule pubescent at maturity; flowers borne on pedicels 2–11 mm long; stigma elongate, 4.0–4.5 mm long ..... *Trichanthera*
   4. Thecae awned with a single, subulate projection 0.3–1.0 mm long at base; capsule glabrous at maturity; flowers sessile or borne on pedicels to 2 mm long; stigma to 1 mm long ..... *Bravaisia*

Morphology

Habit.—*Bravaisia berlandieriana* and *B. grandiflora* vary in habit from shrubs to small trees to 9 m tall. *Bravaisia integerrima* consists of larger trees, to 20 m in height (Fig. 1a), with expansive, often rounded, crowns and usually numerous stilt or prop roots that extend to 8 m above the ground. The base of mature trees varies in diameter from 8 to 200 cm and usually consists of large prop roots and numerous trunks or large branches (Fig. 1b, c). Bark is usually smooth and light in color. The wood is somewhat soft and varies from white to creamy yellow to grayish. Hess (1946) described wood anatomy in the genus. The young stems are quadrate in cross section with four more or less concave surfaces between the prominent corners. Whitish blister-like protrusions, presumably lenticels, are commonly evident on the corners. The young stems are superficially smooth to wrinkled. The mature stems (i.e., those of previous growing seasons) are usually light-colored and wrinkled.

Leaves.—Leaves of *Bravaisia* are opposite-decussate and consist of a well-defined petiole and blade. The petioles are canaliculate on the adaxial surface. The blades are usually somewhat leathery and shiny. They vary in shape from ovate to broadly elliptic to obovate. The surfaces are either glabrous or sparsely pubescent with eglandular trichomes, especially along the midvein. The abaxial surface is often covered with inconspicuous, sparse to dense, sessile, disk-shaped, glandlike structures to 0.05 mm in diameter. These impressed punctations are especially evident in *B. berlandieriana* but are also encountered in the other species. The margin is entire but often so sinuate as to make it appear crenate. Venation is brochidodromous (i.e., the secondary veins join together toward the margin in a series of prominent arches) with up to five orders of veins observable on dried leaves. Sometimes only two to three orders are observable on the more leathery blades of *B. berlandieriana* and *B. grandiflora.* The veins are flush with, slightly impressed into, or slightly protruding from the adaxial laminar surface. The midvein and second order veins protrude prominently from the abaxial surface.

Vesture and Cystoliths.—Unlike many genera of Acanthaceae in which stipitate glandular trichomes are frequent, *Bravaisia* has eglandular trichomes almost exclusively. In the


a
b
c
d
e

genus, readily observable (i.e., with naked eye or dissecting microscope) stipitate glands are found only rarely along styles of *B. integerrima.* The eglandular trichomes are unbranched and consist of 1–4 uniseriate cells. They can occur on most vegetative and reproductive structures. Their presence or absence on the abaxial surface of the corolla is useful in distinguishing the species.

The density of trichomes was found to be somewhat variable within species. Certain specimens of both *B. berlandieriana* (e.g., *Bradburn 1489*) and *B. integerrima* (e.g., *Steyermark 61181*) exhibit a dense pubescence in the inflorescence and on the young stems, whereas in other specimens these structures are largely without trichomes or only sparsely pubescent. Sometimes the young stems of *B. integerrima* are densely pubescent with an even, feltlike vesture consisting of a mixture of eglandular trichomes and sessile glandular punctations. Often as the stems increase in size this covering breaks apart into patches giving the stems a scaly aspect.

In *Bravaisia* cystoliths are best observed on dry, adaxial leaf surfaces. They appear as straight (to slightly curved), protruding, light-colored, lineolate structures up to 0.7 mm long. They are often contiguous with one another, especially when aligned with veins.

INFLORESCENCES.—As in most Acanthaceae, the inflorescence of *Bravaisia* is a thyrse consisting of an indeterminate main axis bearing determinate, lateral axes in the axils of bracts. The determinate, lateral axes are simple dichasia that are usually reduced to a single flower. The number of dichasia per thyrse varies from 3 to 20. In *B. berlandieriana* and *B. grandiflora* the dichasia lack peduncles, and the resulting inflorescence is spicate. In *B. integerrima* the dichasia are borne on distinct peduncles, and the inflorescence is therefore racemose. The modified thyrses of *Bravaisia* are both terminal and axillary from distal leaves; together these form leafy panicles of either spikes or racemes.

Each flower is either sessile or short-pedunculate and subtended by paired, homomorphic bractlets. In *Bravaisia* bractlet form is particularly important because each species can be distinguished by features of the bractlets. The flower(s) and associated bractlets are subtended by a single bract. The bracts are oppositely arranged along the inflorescence.

FLOWERS.—The calyx is deeply five-lobed. The lobes are imbricate and either homomorphic or sometimes somewhat unequal in length. Although Bremekamp (1965) noted that members of the Trichanthereae have obtuse calyx lobes, those of *Bravaisia* vary from rounded to acute to mucronate to apiculate at their apices.

The corolla is campanulate with a short tube, an ampliate throat, and a bilabiate limb. The upper lip of the limb comprises two lobes, and the lower lip consists of three. The lobes are convolute in bud and rounded to emarginate at their apices. Color of the corolla varies from white to bluish white to pinkish with brown and/or yellow markings on the internal surface of the lower lip and throat. Trichomes can be present on internal and external surfaces as well as along the margins of the lobes.

The androecium consists of four fertile epipetalous stamens that are inserted at the base of the corolla throat. They are either included within the throat or exserted several millimeters beyond it. The anthers consist of two equally inserted, parallel thecae, each with a single awn at the base. Thecae vary from glabrous to pubescent with flexuous eglandular trichomes. Three to 15 subsessile, peltate glands, occurring in a band adjacent to the connective on each side of the theca, are usually evident. Pollen of *Bravaisia* has been erroneously described by many workers (Lindau 1895; Raj 1961; Gibson 1974) as diporate. Lindau (1893) described the pollen as a particular type of "Rippenpollen" which he termed "Trichanthereenpollen." Raj (1961) noted that the Trichanthereae are homogeneous in their pollen. An accurate description of the pollen of *B. integerrima* and *B. berlandieriana* (as *B. tubiflora*) was provided by Vasanthy and Pocock (1986). My examination of pollen from each of the species (Fig. 2) reveals it to be consistently dicolporate. The endoapertures (ora) are as-

←

FIGURE 1. Photographs of *Bravaisia.* a, Remnant individual of *B. integerrima* in coastal region of Michoacán, Mexico; b, Base of pruned tree of *B. integerrima* in coastal Guerrero, Mexico, showing numerous adventitious roots; c, Base of *B. integerrima* with divided trunks and prop roots in southern Central America (from photograph at MO); d, Flowers of *B. integerrima* in Guerrero, Mexico, prior to pollination (flower on right) and after pollination (flower on left) showing orientation of stamens, ×1.4; e, Flower and bud of *B. grandiflora* in Chiapas, Mexico, ×1.

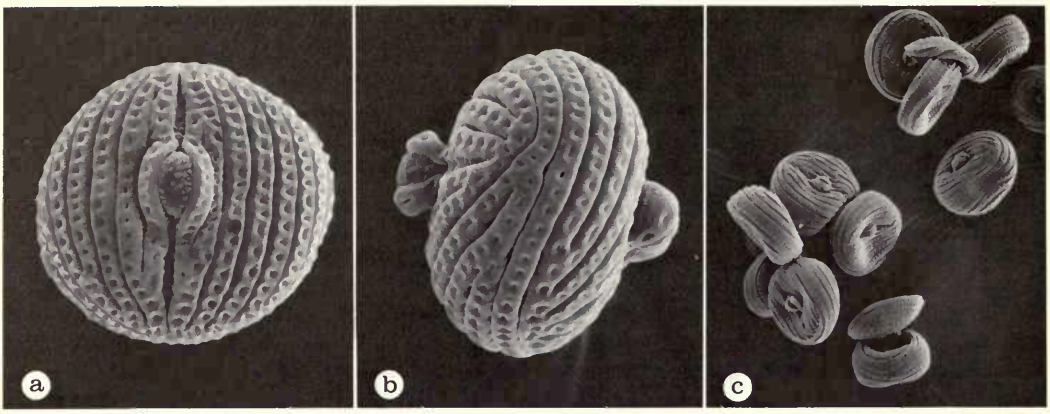


FIGURE 2. Pollen of *Bravaisia*. a, *B. integerrima* (*Daniel 2144*), ×750; b, *B. berlandieriana* (*Cabrera and Ibara 1149*), ×750; c, *B. grandiflora* (*Daniel and Bartholomew 4998*), ×150.

sumed to lie on the equatorial plane of the grain. The grains are partially flattened on the aperturate faces. The compound apertures are centrally positioned on the two flattened faces, 90° out of phase with one another (cf. "rotationally symmetric" in Vasanthy and Pocock [1986]). The pollen might therefore be referred to as "loxodicolporate." The outline of the grain is subcircular to circular when an aperturate face is viewed directly on (Fig. 2a) and elliptical when an inaperturate face is viewed directly on (Fig. 2b). The exine sculpturing consists of a striate pattern of numerous furrows and ridges forming bands of exine oriented in the same direction as the colpi (i.e., perpendicular to one another on the aperturate faces of the grain). Between one and five furrows appear to encircle each grain around its polar periphery. These effectively divide the two identical, but skewed halves of the grain. The ridges, or bands of exine formed by the furrows, each contain a row of centrally positioned foveolae throughout their length. The colpal membranes and the paracolpal furrows are densely studded with granules. Pollen size varies from 54 to 88 μm in diameter (aperturate face). Grains of *B. berlandieriana* and *B. integerrima* are comparable in size (54–66 μm) whereas those of the larger flowered *B. grandiflora* are considerably larger (76–88 μm).

Pollen of *B. grandiflora* from *Daniel and Bartholomew 4998* (Fig. 2c) appears malformed with many of the grains largely or completely collapsed. Three hundred seventy grains of this collection were examined for stainability. Fifty-six (15%) stained completely, 301 (81%) failed to take up any stain, and 13 (4%) took up a small amount of stain. In contrast to the relatively low stainability of pollen from this collection of *B. grandiflora,* 71% of grains examined (364/515) in *B. integerrima* (*Daniel and Bartholomew 4925*) stained completely. Only 29% (151/515) of the grains failed to take up stain; none stained partially.

The gynoecium comprises a bicarpellate, superior ovary, a compound style, and an unlobed, usually curved or coiled stigma. The ovary sits upon a cuplike nectar disc and contains up to 12 ovules.

FRUITS.—The glabrous, explosively dehiscent capsules vary in shape from ovoid to ellipsoid to obovoid. They lack a prominent stalk and have a solid apical beak. Between one and four seeds mature per capsule. These are laterally flattened and subcircular to subellipsoid in outline. Their surfaces are glabrous, smooth, and shiny.

DISTRIBUTION, HABITATS, AND PHENOLOGY

The range of *Bravaisia* extends from western Cuba (ca. 22°30′N), northern Veracruz (ca. 21°30′N) in eastern Mexico, and southern Jalisco (ca. 19°30′N) in western Mexico southward to Colombia and eastern Venezuela (ca. 8°N). The genus is distributed across 44 degrees of longitude, from western Mexico (ca. 105°W) to eastern Venezuela and Trinidad (ca. 61°W). Mexico and Guatemala are the only countries in which all three species are known to occur. *Bravaisia integerrima* is the most widely distributed species and the only one known from South America.

Bravaisia grandiflora has the most restricted distribution, occurring in a region of approximately 24,000 sq. km in southern Mexico, Guatemala, and Belize.

The species occur from sea level to 1,100 m. The plants are usually found along shorelines, streams, and forest edges, or in swamps, marshy areas, and pastures. Each of the species occurs in regions of tropical wet forest. *Bravaisia integerrima* and *B. berlandieriana* also occur in regions of tropical dry forest, mangrove forest (mangal), and other coastal communities. The plants are sometimes a conspicuous, or even dominant, constituent of their biotic communities.

In spite of their similar preferences in habitat, the species of *Bravaisia* appear to be largely allopatric. The ranges of *B. integerrima* and *B. berlandieriana* overlap one another only in southeastern Mexico (Veracruz, Tabasco, and possibly the Yucatán Peninsula). It is not known whether plants of these two species co-occur at any sites. No evidence of hybridization between them was observed based on the collections examined.

Throughout the range of *Bravaisia,* flowering is concentrated during the months of November through April, the dry season in these regions. Fruiting appears to be concentrated during the latter portion of the flowering period.

Infrageneric Relationships

Because the distribution of character states remains unknown for much of the Trichanthereae (see discussion under Infrafamilial Relationships), it is not possible to identify any autapomorphy for *Bravaisia* at present. Therefore, according to strict cladistic principles, monophyly cannot be established for the genus. For purposes of phylogenetic inference, *Trichanthera* is used as the outgroup for determining polarity of character states in *Bravaisia. Trichanthera* appears to be *Bravaisia's* closest morphological ally in the Trichanthereae (see under Infrafamilial Relationships). Character state polarities were established for the six characters listed in Table 1. A diagram (Fig. 3) depicting putative phylogenetic branching patterns among the three species was constructed using character compatibility analysis (Meacham 1981). A hypothetical ancestral taxon, X, exhibiting only plesiomorphic character states, was included in the analysis. The largest clique incorporated all characters ex-

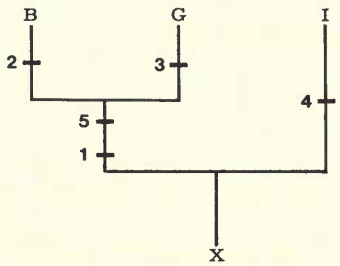


FIGURE 3. Putative phylogenetic branching patterns within *Bravaisia.* Bars indicate apomorphies with numbers corresponding to those in Table 1. B = *B. berlandieriana,* G = *B. grandiflora,* I = *B. integerrima,* and X = a hypothetical ancestor.

TABLE 1. APOMORPHIC AND PLESIOMORPHIC CHARACTER STATES IN BRAVAISIA BASED ON THE OUTGROUP TRICHANTHERA. Numbers correspond to those in Figure 3. I = *B. integerrima,* G = *B. grandiflora,* B = *B. berlandieriana,* and X = a hypothetical ancestor.

Plesiomorphy (−)	Apomorphy (+)	I	G	B	X
1. Dichasia pedunculate with peduncles greater than 1 mm long.	Dichasia sessile or borne on peduncles up to 1 mm long.	−	+	+	−
2. Bractlets shorter than calyx.	Bractlets equal to or longer than calyx.	−	−	+	−
3. Bractlets rounded to acute at apex.	Bractlets apiculate to caudate at apex.	−	+	−	−
4. Corolla pubescent on abaxial surface.	Corolla glabrous on abaxial surface.	+	−	−	−
5. Stamens exserted from throat of corolla.	Stamens included in throat of corolla.	−	+	+	−
6. Mean corolla length greater than 25 mm.	Mean corolla length less than 25 mm.	+	−	+	−

cept character 6 (mean corolla length). *Bravaisia integerrima* is hypothesized to be the sister group of *B. berlandieriana* and *B. grandiflora.* The synapomorphy of short corollas (i.e., character 6) in *B. berlandieriana* and *B. integerrima* appears to represent a parallelism.

Reproductive Biology

Bawa et al. (1985) reported a pollination system of medium-size bees for *Bravaisia integerrima* in a lowland rainforest in Costa Rica. Although I did not perform experimental studies on the reproductive biology of *Bravaisia,* observations on pollination biology were made in the field and gleaned from herbarium specimens.

Flowers of *B. integerrima,* which render the crown nearly white, tend to be abundant for a period of several weeks. Labels on several herbarium specimens indicate that the flowers are somewhat fragrant. *Croat 21533* notes that flowers of this species are visited by small bees and *Hughes and Styles 73* records that the flowers attract bees and hummingbirds. Observations on *B. integerrima* in Colima (*Daniel 2110*), Michoacán (*Daniel 2144*), and Guerrero (*Daniel and Bartholomew 4925*), Mexico during March reveal that the flowers are actively visited by insects. The most abundant visitors in March are honey bees (*Apis mellifera* L.), which use the lower lip as a landing and perching platform while they gather both pollen and nectar. In unpollinated or recently pollinated flowers the didynamous stamens project from the throat, more or less effectively blocking the entrance to the tubular portion of the corolla (Fig. 1d). The style emerges through the upper (dorsal) pair of filaments, overtops them, curves toward the lower lip of the corolla, and positions the stigma directly in front of (distal to) the anthers with the convexly curved and receptive portion facing away from the flower. This arrangement of the androecium and gynoecium would force medium-sized or larger visitors that approach the distal portion of the flower, and follow the colored markings en route to pollen and/or nectar, to contact first the receptive portion of the stigma and then the anthers. Such an arrangement undoubtedly promotes outcrossing. However, geitonogamy likely occurs to a great extent. Bees were observed to visit numerous flowers on a single tree before leaving that individual. In older flowers with pollinated stigmas, the stamens had spread laterally, opening the throat, and the style had curved conspicuously into the throat (Fig. 1d). Pollen removed from hairs on the head and legs of a captured individual of *Apis mellifera* that was visiting *Daniel and Bartholomew 4925* is identical to pollen of *Bravaisia integerrima.* Other visitors to this species in western Mexico include a smaller, native halictid bee, *Halictus* (*Seladonia*) *tripartitus* Cockerell vel aff., on which pollen was not found. Of 10 stigmas observed on flowers of *Daniel and Bartholomew 4925* in Guerrero, seven of them had been pollinated.

In vivo flowers of *B. berlandieriana* were not observed during this investigation. *Bradburn 1476* notes that flowers of this species are frequently visited by hummingbirds.

Bravaisia grandiflora has the largest flowers in the genus. Unlike the androecial arrangement in *B. integerrima,* in this species the stamens are more or less appressed to the dorsal side of the throat and do not block the entrance to the tubular portion of the corolla (Fig. 1e). Nothing is known about visitors to *B. grandiflora.* No visitors to this species were observed in Chiapas, Mexico (*Daniel and Bartholomew 4998*) nor was any fruit production evident. Indeed, only one fruiting collection of this species is known. It remains unknown whether the apparent lack of fruits among individuals of this species is the result of an absence of pollinators or lack of sufficient viable pollen (see discussion under Morphology). However, of 10 stigmas observed on flowers of *Daniel and Bartholomew 4998* in Chiapas, none had adhering pollen.

Taxonomy

Bravaisia DC. Biblioth. Universelle Genève 17: 132. 1838. Type.—*B. floribunda* DC. (=*B. integerrima* (Sprengel) Standley).

Androcentrum Lemaire, Fl. Serrers Jard. Eur. 3:242. 1847 (Jun). Type.—*A. multiflorum* Lemaire (=*B. integerrima*).

Onychacanthus Nees *in* DC. Prodr. 11:217. 1847 (Nov). Type.—*O. cumingii* Nees *in* DC. (lectotype, designated by Leonard [1951]; =*B. integerrima*).

Shrubs to small or medium-sized trees with multiple trunks and usually with numerous stilt roots. Young stems quadrate-sulcate, often with whitish blisters on corners, glabrous or pubescent with eglandular trichomes. Leaves opposite, petiolate; petioles canaliculate; blades usually somewhat leathery, ovate to elliptic to broadly elliptic to obovate, surfaces somewhat shiny, glabrous

or sparsely pubescent with eglandular trichomes, especially along midvein, abaxial surface often covered with inconspicuous, sparse to dense, sessile, disk-shaped glands to 0.05 mm in diameter (punctate-glandular), margin entire to sinuate-crenate, usually somewhat revolute. Inflorescence of axillary and terminal, sessile or pedunculate dichasia (usually reduced to one flower) borne in axil of a bract (or terminal dichasia borne in axil of two bracts) and arranged in short spicate or racemose axes which form terminal panicles; flowers sessile or short-pedicellate in axil of two isomorphic bractlets. Bracts opposite, sessile or petiolate, variously shaped. Bractlets variously shaped, rounded to acute to apiculate to caudate at apex. Calyx deeply five-lobed; tube 0.5–2.0 mm long; lobes imbricate, often turning dark green or brown on dried material, ovate to elliptic to suborbicular to obovate. Corolla white, bluish white, or pinkish, glabrous or pubescent on external surface, sometimes bearded within; tube shorter than throat; limb bilabiate with upper lip two-lobed, lower lip three-lobed, lobes convolute in bud, ovate to elliptic to suborbicular to obovate, rounded to emarginate at apex. Stamens four, didynamous, inserted at base of corolla throat, included or exserted from throat; filaments densely pubescent at base, sparsely pubescent (to nearly glabrous in *B. integerrima*) distally; anthers bithecous, thecae equally inserted, parallel, glabrous to sparsely pubescent with eglandular trichomes, usually with peltate glands 0.1–0.2 mm in diameter evident as well, rounded at apex, awned at base with a single, subulate projection 0.3–1.0 mm long; pollen loxodicolporate, the surface striate-foveolate. Ovary situated on a distinct or indistinct disc 0.7–1.0 mm tall; ovules to 12; style exserted from throat of corolla, glabrous (rarely sparsely pubescent near base); stigma usually coiled or curved, up to 1 mm long. Capsule ovoid to ellipsoid to obovoid, estipitate (i.e., solid basal portion less than 0.5 mm long), with a solid apical beak 1.2–2.1 mm long; retinacula 2–4 mm long. Seeds one to four per mature capsule, brown, strongly laterally flattened and subcircular in outline to only slightly flattened and subellipsoid, glabrous, surface smooth and shiny.

Key to the Species of *Bravaisia*

1. Bractlets apiculate to caudate at apex; corolla 27–47 mm long ..... 2. *B. grandiflora*
1. Bractlets rounded to acute at apex; corolla 15–25 mm long.
   2. Inflorescence racemose, dichasia borne on peduncles (1.0–)1.5–6.0(–13.0) mm long; bractlets linear to triangular to suborbicular, 1.6–5.0 mm long, shorter than calyx; corolla externally glabrous (margins of lobes ciliate, however), tube 1.7–3.2 mm long, usually not well differentiated from throat; style 7–13 mm long; seeds 0.5–1.2 mm thick ..... 1. *B. integerrima*
   2. Inflorescence spicate, dichasia sessile (rarely borne on peduncles to 1 mm long); bractlets obspatulate (i.e., constricted distally) to hourglass shaped (i.e., constricted medially) to spatulate (i.e., constricted proximally), (5–)7–15(–20) mm long, equal to or usually longer than calyx; corolla exernally pubescent, tube 4–8 mm long, clearly differentiated from throat; style 14–21 mm long; seeds 1.8–2.6 mm thick ..... 3. *B. berlandieriana*

1. Bravaisia integerrima (Sprengel) Standley, Contr. U.S. Natl. Herb. 23:1335. 1926.

Amasonia integerrima Sprengel, Syst. Veg. 2:765. 1825. TYPE.—COLOMBIA. "Ad. fl. Magdalen. Bertero." fide protologue; "ex Amer. meridionali h. Bertero Mr Balb. 1822" (G-DC!, photos F, MO, US). Leonard (1951) indicated this specimen as the type material of *A. integerrima* and incorrectly noted its being at G-DEL. Because Sprengel cited a more precise locality for Bertero's collection than that noted on the specimen at G, it is possible that he had a specimen with a different label in his herbarium (i.e., the holotype). The specimen at G is possibly an isotype. A Bertero collection from "Sta. Martha" labelled as *A. integerrima* Spr. at P(!) and as *Bignonia bibracteata* at G-DC(!) and MO ex hb. Bernhardi(!) likely does not represent isotype material since Santa Marta is about 80 km to the northeast of the Río Magdalena. Although the major portion of Bertero's collections are at TO (G. Forneris, in litt.), there are no specimens under either *Amasonia integerrima* or *Bignonia bibracteata* currently at that institution (G. Forneris, in litt.). Sprengel's herbarium was dismembered after his death, and a considerable portion of it was destroyed at B.

Bravaisia floribunda DC. Biblioth. Universelle Genève 17:132. 1838. TYPE.—VENEZUELA. Caracas, *Vargas s.n.* (Holotype: G-DC!; isotype K!). Although initial publication of this species is usually given as occurring in DC. Prodr. 9:240, 1845, de Candolle's earlier treatment fulfills all of the requirements of Article 42 of the ICBN for a *descriptio generico-specifico*. If, in fact, the latter publication were to be accepted as the initial publication of this species, the name would be illegitimate under Article 63.1 of the ICBN since *Amasonia integerrima* Sprengel (the epithet of which ought to have been adopted) was cited as a synonym.

Androcentrum multiflorum Lemaire, Fl. Serr. Jard. 3:242. 1847. TYPE.—MEXICO. Galeotti (Holotype unknown). In the protologue Lemaire drew his description from a dried specimen of a Mexican plant sent by Galeotti. The disposition of Lemaire's herbarium is not known. Galeotti's only known collections of *Bravaisia* came from Oaxaca (one collected at "Tututepeque" in May and numbered *510M* at BR and one collected at "Lacs de Tututepeque" in April and also numbered *510M* at BR, F, GH, MO, NY, UC, US). One of these collections undoubtedly represents the type material.

Onychacanthus cumingii Nees *in* DC. Prodr. 11:217. 1847. TYPE.—Nees cited the following syntypes: a Pavón collection from Peru (in de Candolle's herbarium), *Cuming 1307* from Central America (in the herbaria of Bentham and Hooker), and a specimen labelled as *Ruellia arborescens* Pavón (in Moricand's herbarium). Leonard (1951) effectively lectotypified this species when he indicated that the type was collected in Peru by Pavón and deposited in the de Candolle herbarium. I was unable to locate this collection at G-DC; however, isolectotypes were seen at BM and P. The specimen at P is attributed to Peru. One of the labels on the isolectotype at BM gives the "name" *Ruellia arborescens* and the locality "NE" (i.e., Nueva España or Mexico). This "name" was applied to a Mexican specimen (at MA) of what is here considered to be *B. integerrima* by Sessé and Mociño. The lectotype material was undoubtedly collected by Sessé and Mociño in Mexico and wrongly attributed to Peru, from which region the plant is not known to occur. See McVaugh (1987) for a discussion of certain Sessé and Mociño collections erroneously believed to have been collected in Peru.

Onychacanthus speciosus Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854:131. 1854. TYPE.—COSTA RICA. Puntarenas: La Barranca near Puntarenas, Feb. 1847, *A. Oersted 10624* (Lectotype: C!). In the protologue Oersted mentions collections from Costa Rica and Nicaragua. At C there are three Oersted collections of this species, two from La Barranca in Costa Rica and one from Volcán Mombacho in Nicaragua. From among these syntypes, the collection cited above is here chosen as the lectotype.

Onychacanthus arboreus Karsten, Fl. Columb. 2:111. 1865. TYPE.—VENEZUELA. "Habitat regiones montuosas calidas Venezuelae in provincia Caracas prope oppida Victoria et San Sebastian observata." The location of Karsten's herbarium is unknown. I have not seen any specimens that might represent type material of this species. Stafleu and Cowan (1979) note that important sets of plants collected by Karsten are to be found at LE and W. Neither of these herbaria reports having material with the above name and locality. The illustration provided in the protologue pertains to *B. integerrima*.

Tree to 20 m tall; numerous stilt or prop roots often present around the base; main trunk divided at or above the base into several prominent trunks; bark light gray to dark gray-brown, sometimes mottled, smooth or slightly warty; crown spreading, often somewhat rounded. Younger stems glabrous, farinose-puberulent with trichomes to 0.05 mm long, or pubescent with flexuose to ascendant-appressed or retrorse-appressed trichomes 0.1–0.5 mm long, the youngest growth sometimes densely pubescent with flexuose to appressed trichomes up to 1.5 mm long. Leaves with petioles to 90 mm long; blades ovate to elliptic to broadly elliptic to obovate-elliptic, 30–305 mm long, 11–157 mm wide, 1.4–3.6 times longer than wide, rounded to acute to attenuate at base, (rounded to) acute to acuminate at apex, surfaces glabrous or with scattered trichomes along veins on abaxial surface, abaxial surface usually punctate-glandular, adaxial surface somewhat darker than abaxial surface. Inflorescence racemose; dichasia (3–)6–10(–20) per raceme, borne on peduncles (1.0–)1.5–6.0(–13.0) mm long; flowers sessile (or borne on pedicels to 2 mm long); rachis densely pubescent with eglandular trichomes 0.05–0.5(–1.0) mm long. Bracts linear to linear-subulate to triangular to ovate, lowermost rarely petiolate, 2–14 mm long, 0.7–4.0 mm wide, abaxial surface pubescent like rachis, sometimes punctate-glandular. Bractlets linear to triangular to suborbicular, 1.6–5.0 mm long, shorter than calyx, 1.0–2.5 mm wide, rounded to acute at apex, abaxial surface pubescent like rachis to glabrous, sometimes punctate-glandular, margin ciliate with straight to flexuose trichomes to 0.3 mm long. Calyx 3–10 mm long; lobes sometimes unequal in length, ovate to elliptic to suborbicular to obovate-elliptic, 2–8 mm long, rounded to acute at apex, pubescent like bractlets, sometimes punctate-glandular. Corolla white with brown and yellow markings on inner surface of lower lip, 15–22 mm long, externally glabrous; tube 1.7–3.2 mm long (usually not well differentiated from throat); throat 5.5–10.0 mm long, 5.5–11.0 mm in diameter near midpoint; limb 17–27 mm in diameter with lobes 6–12 mm long, lobes sparsely ciliate on margin. Stamens exserted from throat, shorter pair 7–9 mm long, longer pair 9–11 mm long; filaments maroon; thecae maroon, 2.1–3.2 mm long including basal awn, sparsely pubescent to glabrous; pollen 53.9–61.3 μm in diameter. Style white, 7–13 long, glabrous (rarely sparsely pubescent near base with eglandular trichomes to 0.7 mm long and occasionally with stipitate glands up to 0.1 mm long as well). Capsule ellipsoid to obovoid, 5–13 mm long, glabrous at maturity (rarely sparsely pubescent near apex when immature); retinacula to 3.5 mm long. Seeds one (to four), subcircular, strongly laterally flattened, 3–5 mm long, 2.8–4.0 mm wide, 0.5–1.2 mm thick, surfaces glabrous, smooth, shiny (Fig. 4).

PHENOLOGY.—Flowering and fruiting September through May, also in July.

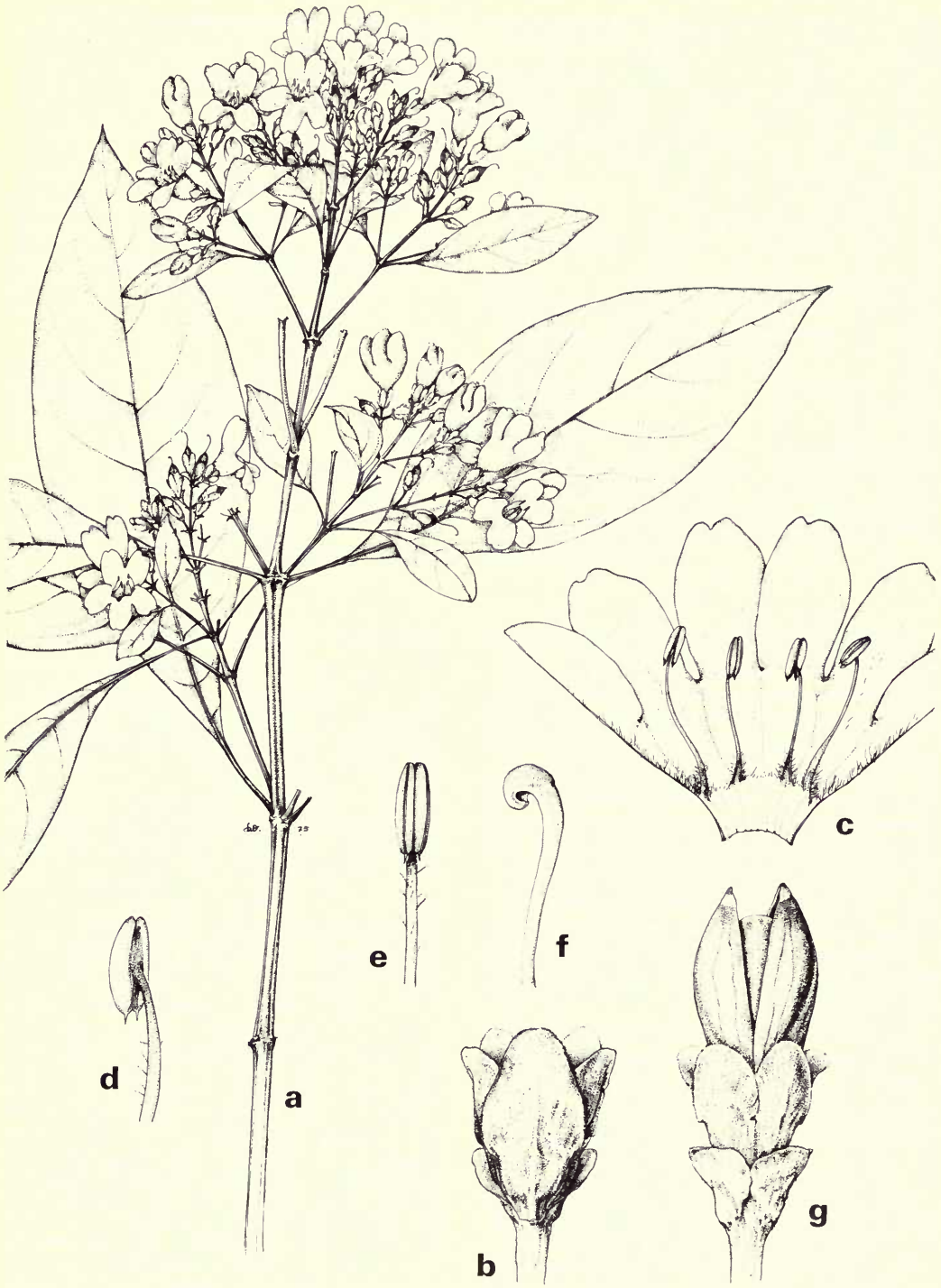


FIGURE 4. *Bravaisia integerrima* (*McVaugh 22884*). a, Habit, ×½; b, Bractlets and calyx, ×3.5; c, Corolla cut open showing epipetalous, didynamous stamens, ×2; d, Distal portion of filament and anther, posterior side, ×5; e, Distal portion of filament and anther, anterior side, ×5; f, Distal portion of style and stigma, ×5; g, Dehiscing capsule with subtending calyx and bractlets, ×3.5. Drawing by Karin Douthit for McVaugh's *Flora Novo-Galiciana;* copyright reserved to the University of Michigan Herbarium, used with permission.

FIGURE 5. Distribution of *Bravaisia integerrima.*

DISTRIBUTION.—West-central through southeastern Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, and Trinidad (Fig. 5). The plants occur along streams and forest edges, in pastures, and in swamps in regions of tropical dry forest, tropical wet forest, and mangrove forest, at elevations from near sea level to 1,100 m; most collections were made at elevations below 300 m. Associates include species of *Brosimum, Bursera, Dialium, Ficus, Guazuma, Heliocarpus, Inga, Lonchocarpus, Ocotea, Orbignya, Pithecellobium,* and *Spondias.* The plants are often abundant and sometimes become the most common understory tree.

All of the names listed above as synonyms of *B. integerrima* were similarly treated by Leonard (1951) with the exception of *Androcentrum multiflorum.* Standley (1926) noted that specimens referred to *A. multiflorum* that he had seen appeared to be conspecific with *B. integerrima.* Although the holotype of this species is not known with certainty, probable type material (i.e., *Galeotti 510M*) is referable to *B. integerrima.*

Bravaisia integerrima differs from the other species of the genus by its externally glabrous corollas, exserted stamens, and racemose inflorescences with the dichasia borne on peduncles 1–13 mm long.

Considering the wide distribution, arboreal nature, unusual form, and occasional local abundance of *B. integerrima,* it is not surprising that numerous local names have been recorded for this species. These are: "árbol de lluvia" (*Elias 974*), "charote" (*Lopez-Palacios 1810*), "chorote" (*Bunting 9150*), "cien patos" (*Wendt et al. 3114*), "cien-pied" (*Williams 8913*), "cintopie" (*M.A.M.A. 677*), "curta" (*Smith 123, 270*; *Pittier 7760*), "curte" (*Pittier 7727*), "jigger tree" (*Britton et al. 1099*), "jigger wood" (*Chalmers s.n.*; *Marshall 12474*), "mangle" (*Steyermark 62161*), "mangle blanco" (*Alexander 74-16*; *Brenes 6600, 6600a*; *Chaves 184*; *Englesing 147*; *Hartshorn 1172, 1294*), "mangle de agua" (*Cooper and Slater 269*), "mangle llanero" (*Molina R. 2130*), "naranjillo" (*Bernardi 1174, 6311, 6903*; *John 335*; *Pittier 7727, 11449*; *Steyermark 89202*; *Williams 12341, 12904*; *Wurdack and Monachino 39712*), "palo blanco" (*González T. 46*; *Langlassé 831*; *Villegas 247*), "palo de agua" (*Brenes 6660a*; *Dugand 13, 412, 542, 580*; *Dugand and Jaramillo 4094*; *Dunlap 23*; *Elias 444, 487, 1265, 1507*; *Jiménez L. 367*; *Romero 34*; *Soto and Ramón de Soto 759*), "pata de gallo" (*Cedillo T. 736*), "sancarano" (*Curran 222*), "sancho-araña" (Curran 1929), "white mangue" (*Chalmers s.n.*), "yaga-zee" (*Seler and Seler 1609*).

Bravaisia integerrima does not appear to have significant economic value. Hess (1946:17) reported that "the wood has no special uses but appears suitable for cheap construction lumber or box boards." Curran (1929:18) noted that some of the main branches "are large enough to be utilized for timber. Wood nearly white, odorless and tasteless, moderately soft, easy to work, not readily discolored or attacked by insects when left on the ground after logging." Curran (1929) further notes that the wood is appropriate for packing crates. Others (Record 1929; *Williams 12904*) report that the wood is not used. *Steyermark 61181* indicates that the root is cooked in guarapo (a fermented beverage made from either sugar cane or pineapple) and used by the "curiosos" for pains. *Chazaro B. and Dominguez 2158* note that the flowers are melliferous. The species is sometimes cultivated in tropical botanic gardens (e.g., Martinique and Caracas) and is reported to be planted along streets in South America.

Representative Specimens Examined.—Colombia. Atlántico: near Puerto Colombia, *Dugand 13* (F); "Convento" near Galapa, *Dugand 412* (F); Arroyo de Piedras, *Dugand 580* (F, US); Juanmina, *Dugand and Jaramillo 4094* (US); Galapa, *Elias 444* (US); Sabanalarga, *Elias 487* (US); region of Barranquilla, *Elias 1265* (A, F, US), *1507* (F, US). Bolívar: vicinity of Estrella, Caño Papayal, Lands of Loba, *Curran 308* (GH, US); 1 km de Buenavista, camino entre Carrizal y Buenavista, *Forero and Jaramillo 500* (F, MO, NY, US); Morrocoquiel, on Río Sinú, *Pennell 4697* (F, GH, K, MO, NY, US). Guajira: near Barrancas, on Río Ranchería, *Haught 3989* (F, K, NY, P, US). Magdalena: vicinity of Santa Marta, *Romero 34* (MO), *Smith 1869* (A, BM, BR, F, G, GH, K, LL, MICH, MO, NY, P, PH, UC, US); Ciénaga, *Romero 980* (US). Department not determined: Sabanilla lagoon, *Dugand 83* (F); El Pajar forest, *Dugand 542* (F, G). Costa Rica. Alajuela: San Francisco y San Pedro de San Ramón, *Brenes 6600* (F); Santiago de San Ramón, *Brenes 6660a* (NY); llanura de San Carlos, near Los Angeles, *Molina R. et al. 17645* (F, GH, NY); Aguas Claras, 40 km N of Pan Am. Hwy., *Utley and Utley 3987* (CAS, F, MICH, MO, NY, WIS). Guanacaste: ca. 11 km N of La Cruz, *Liesner 4847* (F, MO); above Río Las Cañas, H. Granadilla, *Dodge and Thomas 6393* (GH, MO); Colonia Carmona, *Jiménez L. 367* (US); Río Congo, entre Río Lagarto y Limonal, *Jiménez M. 301* (F, G, US); bords des chemins a Nicoya, *Tonduz 13884* (G, K, P). Heredia: slopes of Volcán Barba, *Bawa 305* (MO); Puerto Viejo, *Biolley 7368* (BM, US); along Sarapiquí rd., ca. 10 km N of San Miguel, *Hartshorn 1172* (MO). Puntarenas: vicinity Palmar Norte de Osa, *Allen 5714* (BM, DS, F, GH, US); entre playas Jacó y Herradura, *Jiménez M. 1702* (BM, F, US, WIS); La Barranca, *Oersted 10633* (C). San José: Turubares près de San Mateo, *Biolley 7105* (BM, P, US), *16134* (G, MEXU, MO, US). El Salvador. La Libertad: coastal hwy. W of La Libertad, *Allen 7201* (F, LL, MICH, NY, US). San Miguel: W of Hacienda San Román, ca. 13 km S of Lake Olomega, 13°10′N, 88°04′W, *Tucker 864* (F, K, MICH, UC, US). Usulután: La Concordia, *Calderón 2138* (GH, US). Guatemala. Department not determined: Guaumitul (sp?), *Bernoulli and Cario 2042* (K, MO). Honduras. Choluteca: 4 km SO de Marcovia, *Alexander 74-16* (MO). Comayagua: along Río Humuya, 1 km SE of Comayagua, *Hazlett 1189* (MO). Mexico. Chiapas: cerca de Pichucalco, *Gómez-Pompa 711* (MEXU); 20 km NO de Randales, *González Q. 3496* (ENCB, MICH); Mt. Ovando, Escuintla, *Matuda 16218* (MEXU, US). Colima: along Hwy. 200, Club Santiago Golf Course, 3.0 mi (4.8 km) NW of Santiago, *Daniel 2110* (ASU, CAS, ENCB, MEXU, MICH, NY); environs de Cuyutlán, *Diguet s.n.* (MICH, P); Mpio. Tecomán, 5 km O de Chenchopa, *Rzedowski 15397* (ENCB, MEXU, TEX); Costa Rica, 15 km SE de Manzanillo, *Soto and Ramón de Soto 759* (CAS, MEXU, RSA). Guerrero: along Hwy. 200 between Petatlán and Tecpan, just SE of Juluchuca, *Daniel and Bartholomew 4925* (CAS, DUKE, K, MEXU, MICH, NY); Rives du Rio Coyaquilla, *Langlassé 831* (G, GH, K, MICH, P, US); La Lagunilla, *Nelson 7001* (GH, NY, US). Jalisco: 10 km antes de La Huerta, *Ramirez V. 19* (IBUG); Barra de Navidad a 123 kms, *Puga 2916* (ENCB, IBUG). Michoacán: along Hwy. 200 between turns to Coahuayana and Aquila, 2.5 mi (4.0 km) N of Río El Ticuiz, *Daniel 2144* (ASU, CAS, ENCB, MEXU, MICH, NY); ca. 8 km W of Apatzingán, *McVaugh 22884* (ENCB, MICH); alrededores de El Habillal, 15 km O de Playa Azul, *Villegas 247* (ENCB). Oaxaca: near Huilotepec, *Alexander 268* (MEXU, MICH, NY); Distr. Juchitán, cerca de Bernal, al NE de Chahuites, *Cedillo T. 736* (MEXU); from Jamiltepec to Río Verde, *Nelson 2375* (GH, US); 15 km de Puerto Escondido en el camino a Puerto Angel, *Pennington and Sarukhan K. 9491* (A, K, MEXU, NY); Huilotepec, *Seler and Seler 1609* (GH). Tabasco: Mpio. Cárdenas, KM 21 de la carretera Cárdenas-Coatzacoalcos, *Magaña and Zamudio 128* (CAS, ENCB, IBUG, MEXU, MO); Mpio. Cárdenas, Escuela, *M.A.M.A. 677* (MEXU). Veracruz: ca. 40 mi (64 km) N of Chachalacas, *Davis and Kincaid 55-7* (TEX); Mpio. Hidalgotitlán, 1 km al S del Poblado 7, 17°19′N, 94°31′W, *Wendt et al. 3114* (CAS, DAV, ENCB, F, MICH, NY, TEX, WIS); Fortuño, Coatzacoalcos River, *Williams 8913* (A, CAS, DS, F, GH, MICH, UC, US). Yucatán: without locality, *Johnson s.n.* (NY). State not determined: without locality, *Haenke 1439* (F), *Sessé, Mociño et al. 275* (F), *2147* (F). Nicaragua. Boaco: along carretera 7, between Boaco cutoff, Dept. Chontales, and Tipitapa, Dept. Managua, *Bunting and Licht 740* (F, NY, US). Chinandega: Palo Blanco, *Shannon 5005* (F, G, GH, K, NY, US). Chontales: between Santo Tomás and Villa Somozo, near border with Depto. Zelaya, *Bunting and Licht 1101* (BM, F, WIS). Granada: Volcán Mombacho, *Baker 2363* (A, F, G, GH, K, MO, POM, UC, US); *Oersted 10634* (C). Jinotega: al NE de Wiwilí, camino entre El Carmen y Wamblán, a lo largo del Río Coco, *Araquistain and Castro 1883* (TEX). León: KM. 52, carretera vieja a León, La Paz Centro, 12°20′N, 86°42′W, *Moreno 6595* (MO). Managua: Managua, *Chaves 184* (US); 5 km SE of San Francisco NE of Lago de Managua, *Hughes and Styles 73* (MEXU); Cuesta del Coyol, Pan Am. Hwy., ca. 60 mi (96 km) N of Managua, *Williams et al. 25070* (F, LL, NY, US). Zelaya: bank of Morcielago Creek, region of Braggman's Bluff, *Englesing 147* (F, K); La Esperanza, Río Grande, *Molina R. 2130* (F). Department not determined: Sierra de Managua, *Garnier 1003* (US); without locality, *Wright s.n.* 1853–56 (GH, P, US). Panama. Bocas del Toro: vicinity of Almirante, *Cooper 25a* (F, GH, MO, NY, US); Changuinola Valley, *Dunlap 23* (F); 10–15 mi (16–24 km) inland (S) from mouth of Río Changuinola, *Lewis et al. 886* (MO, US, WIS). Chiriquí: Progresso,

Cooper and Slater 269 (F, NY, US); Burica Peninsula, Rabo de Puerco, 8 km W of Puerto Armuelles, *Croat 21966* (CAS, DAV, F, MO, NY). TRINIDAD AND TOBAGO. St. Patrick: Erin, *Broadway 2555* (BR, F, MICH, US). Victoria: Moruga, La Fortune Trace, *Broadway 7919* (K, NY). County undetermined: Southern Watershed Reserve, *Britton et al. 1099* (GH, NY, US), *Marshall 12474* (K, NY); Belmont, *Broadway s.n.* (NY); Catshill Reserve, *Chalmers s.n.* 29.3.63 (K, US). VENEZUELA. Anzoátegui: Cantaura, *Smith 123* (US); vicinity of confluence of Río León with Río Zumbador, NE of Bergantín, *Steyermark 61181* (F, K, US). Aragua: between Maracay and S. Mater., *Alston 6057* (BM, F, K, NY, US); Maracay, *Linden 441* (G, P); La Trinidad de Maracay, *Pittier 5807* (F, MO, NY, P, US); Magdalena y El Tocorón, *Williams 12341* (F, US). Barinas: La Libertad, bosques del Cachicamo, *Bernardi 1174* (G, NY); orillas del Río Masparro, *Bernardi 6311* (G). Bolívar: SE of Cerro Pichacho, N of Las Nieves, 45 km N of Tumeremo, *Steyermark 89202* (NY, US); El Palmar, *Williams 12904* (A, F, K, UC, US). Carabobo: between Valencia and Maracay, *Pittier 7727* (GH, US). Delta Amacuro: Serranía Imataca, 2–6 km SE of Río Guanamo, *Wurdack and Monachino 39712* (NY). Distrito Federal: vicinity of Caracas, *Bailey and Bailey 1107* (US), vicinity of Maiquetía, *Gentry and Morillo 10325* (MO, NO, NY, US); Puerto La Cruz, *John 335* (US); El Paují, road Caracas-La Guaira, *Pittier 13358* (G, NY, PH). Guárico: vicinity of El Sombrero, along rd. to Calabozo, *Pittier 11449* (A, G, GH, K, NY, P, US). Lara: between Humocaro Alto and Humocaro Bajo, *Steyermark 55551* (F, US). Miranda: between Carenero and Chirimena, along Quebrada del India, *Steyermark and Carreño E. 106903* (F, P, US). Monagas: ca. 7.5 km SSE of San Felix, *Pursell et al. 8446* (NY, US); Caicara, *Smith 270* (NY, US); Caripe, N side of Río Caripe, coffee hacienda, *Steyermark 62161* (F, MO, NY, US). Sucre: Sabilar (Carr. Cumaná-S. Juan Macarapana), *Cumana C. 248* (MEXU); Distr. Benítez, along Caño Ajíes, N of Ajíes, 10°28'N, 63°05'W, *Steyermark et al. 121317* (MO). Trujillo: Alcabala de La Concepción, *Delgado 349* (US); between Motatan and Valera, *Alston 6391* (BM). Yaracuy: Colonia Yumare, *Bernardi 6903* (G, K, NY). Zulia: Dtto. Perijá, KM 25 al SE de San José, *Bunting 5544* (NY, US); Dtto. Bolívar, entre Campo Lara y Piedras Blancas, *Bunting 9150* (NY, US); Dtto. Mara, alrededores de Campamento Carichuano (de Carbozulia), *Bunting 10009* (US); vicinity of Perijá, *Tejera 113* (GH, US). State undetermined: without locality, *Funcke and Schlim 441* (BM), *Otto 538* (K, P). COUNTRY UNDETERMINED. Central America (printed label on specimen at F ex K says western South America; date of collection given as 1831 on specimen at K; label on specimen at BM notes collection in Costa Rica in 1832), *Cuming 1307* (BM, CGE, F, K).

2. Bravaisia grandiflora J. D. Smith, Bot. Gaz. 33:255. 1902. TYPE.—GUATEMALA. Alta Verapaz: "In silvis ad Sachicha," Apr. 1901, *von Tuerckheim 7924* (Holotype: US!).

Bravaisia proxima S. F. Blake, Contr. Gray Herb. 52:96. 1917. TYPE.—BELIZE: upper Moho River, 16 Mar. 1907, *M. E. Peck 730* (Holotype: GH!; photo: NY!).

Shrub to understory tree to 9 m tall; trunk to 20 cm in diameter; bark light-colored, smooth. Younger stems glabrous or sparsely pubescent with flexuose to retrorse- or antrorse-appressed trichomes to 1.4 mm long. Leaves with petioles to 40 mm long; blades elliptic to obovate, 30–190 mm long, 10–75 mm wide, 2.1–4.5 times longer than wide, attenuate at base, acuminate to acute (sometimes aristate) at apex, surfaces glabrous or pubescent along veins on abaxial surface, abaxial surface sometimes punctate-glandular. Inflorescence spicate; dichasia one to five (commonly three) per spike, sessile; flowers sessile; rachis pubescent with flexuose to ascendant-appressed, sometimes golden trichomes 0.1–1.1 mm long, sometimes punctate-glandular. Bracts petiolate or narrowed at or near base and abruptly expanding into lanceolate to narrowly elliptic to oblanceolate lamina, lowermost sometimes ovate to elliptic and uppermost sometimes widest at base and narrowed distally, 2.5–15.0(–23.0) mm long, 1–8 mm wide, pubescent like rachis near base, often glabrous above, sometimes punctate-glandular. Bractlets triangular to orbiculate to somewhat squarish, 3–8 mm long, shorter than calyx, 1.5–4.0 mm wide, prominently apiculate to caudate at apex, the abaxial surface pubescent like rachis (often only sparsely so) and sometimes punctate-glandular, margin ciliate (at least near the apex) with mostly straight trichomes 0.05–0.5 mm long. Calyx 5.0–10.5 mm long; lobes obovate to elliptic, mucronate to apiculate at apex, abaxial surface densely puberulent with ascendant trichomes 0.05–0.20(–0.50) mm long and sometimes punctate-glandular, margin densely ciliate with straight to flexuose trichomes to 1 mm long. Corolla purplish white or pinkish with yellow markings in throat, 27–47 mm long, externally pubescent with trichomes 0.3–0.7 mm long; tube 6–13 mm long; throat 12–22 mm long, 7.5–13.0 mm in diameter near midpoint; limb 22–40 mm in diameter with lobes 7–18 mm long, lobes ciliate. Stamens included in throat or the longer pair slightly emergent, shorter pair 9–14 mm long, longer pair 11–19 mm long; thecae 3.0–4.5 mm long including basal awn, pubescent with flexuose or twisted trichomes; pollen 75.9–88.2 μm in diameter. Style 20–29 mm long, glabrous. Capsule ovoid, 10 mm long, glabrous. Seeds not seen (Fig. 6).

PHENOLOGY.—Flowering January through April; fruiting in June.

DISTRIBUTION.—Southern Mexico, northern Guatemala, and southern Belize (Fig. 7). The plants occur along streams and at the edges of forests in regions of tropical wet forest at elevations from 90 to 1,000 m.

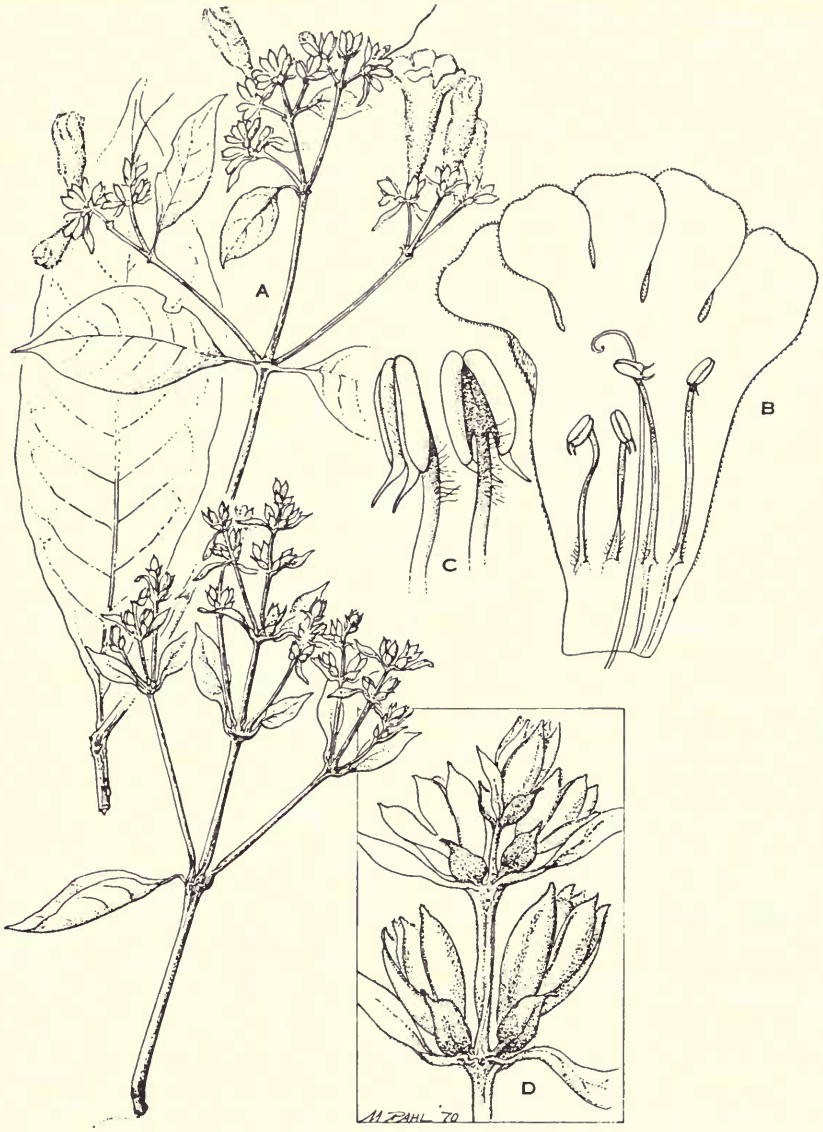


FIGURE 6. *Bravaisia grandiflora* as illustrated by figure 75 in Gibson's treatment of Acanthaceae in *Flora of Guatemala;* copyright Field Museum of Natural History, used with permission.

Gibson (1974) was the first to synonymize *B. proxima* with *B. grandiflora.* The species is readily distinguishable by its large, pubescent corollas and apically apiculate to caudate bractlets. The local name "boc-ché" (Quecchí dialect) has been noted from Guatemala (*Johnson 187*) for this species.

ADDITIONAL SPECIMENS EXAMINED.—BELIZE. Toledo: Bolo Camp, upper reach of Golden Stream River, *Gentle 4555* (LL); along Temash River, *Lamb 58* (F); Blue Creek, *Whiteford 3219* (BM, MEXU, MO, NO). District undetermined: Jacinto Hills, *Schipp 1259* (A, BM, F, G, GH, MICH, MO, NY). GUATEMALA. Alta Verapaz: Chama, along Río Salba, *Johnson 187* (US); 8–10 mi (13–16 km) NW of Cubilguitz, *Steyermark 45031* (A, F, LL, US); Yaxcabnal, *von Tuerckheim 8259* (A, GH, K, MO, NY, US). Petén: Santa Isabel, *Contreras 6694* (K), *6695* (K, US); La Cumbre, KM 155 of Cadenas Rd., Chacalte Abajo, *Contreras 10563* (ENCB, LL, RSA); Dolores, en la orilla del Río Machaquilla a Km. 93, *Tún Ortíz 1642* (F, MO, NY, US). Izabal: El Estor, *Contreras 11383* (US); between Cienaga and Pto. Méndez along Petén-Río Dulce Hwy., *Tún Ortíz 2351*

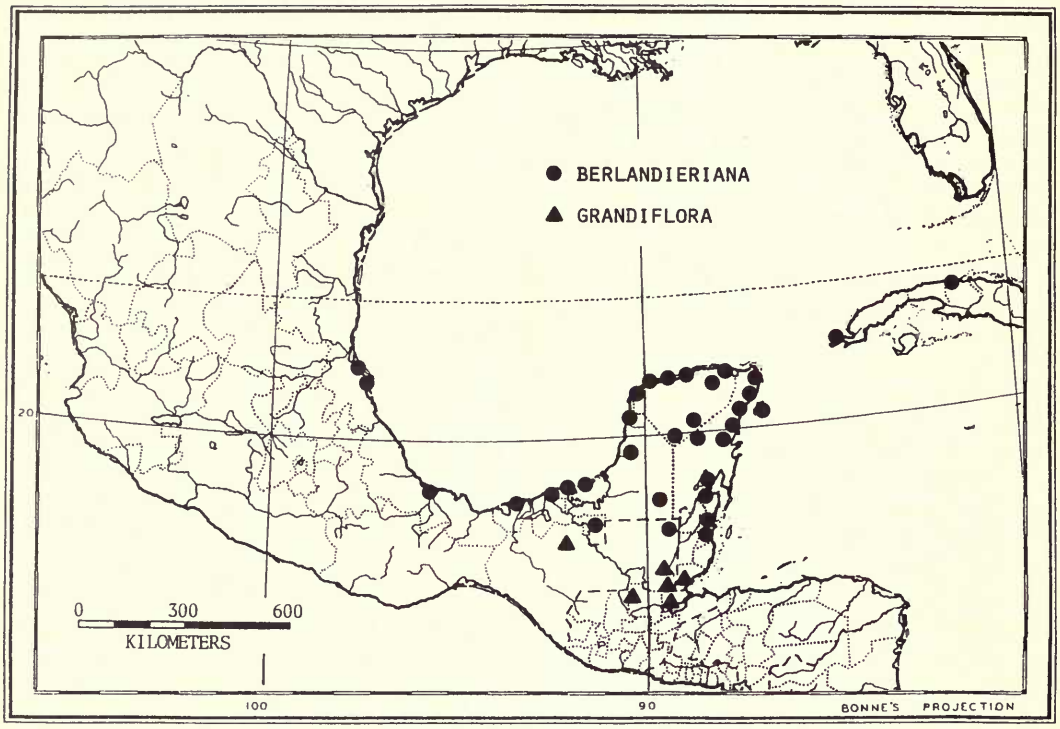


FIGURE 7. Distribution of *Bravaisia grandiflora* (triangles) and *B. berlandieriana* (dots).

(BM, F, MICH, US). Department undetermined: eastern portions of Vera Paz and Chiquimula, *Watson 240* (F, GH, US). MEXICO. Chiapas: Mpio. Palenque, Agua Azul, *Breedlove 49859* (CAS), *Daniel and Bartholomew 4998* (ASU, CAS, DUKE, ENCB, F, K, MEXU, MICH, MO, NY, TEX, US), *Ventura A. 20001* (CAS).

3. **Bravaisia berlandieriana** (Nees) T. F. Daniel, comb. nov.

Onychacanthus berlandierianus Nees *in* DC. Prodr. 11:217. 1847. TYPE.—MEXICO. Veracruz: vicinity of Laguna de Tamiahua, S of Tampico, Tamaulipas, *J. L. Berlandier 108* (Holotype: G!; isotypes: BM!, P!).

Bravaisia tubiflora Hemsley *in* Hook. Icon. Pl., ser. 3, 16: t. 1516. 1886. TYPE.—MEXICO. Quintana Roo: Cozumel Island, 25 Apr. 1885, *G. Gaumer 52* (K!).

Shrub to tree to 7.5 m tall; trunk to 8 cm in diameter. Younger stems pubescent with ascendant-appressed to ascendant to erect to flexuose trichomes 0.1–1.0 mm long or nearly glabrous. Leaves with petioles to 35 mm long; blades ovate-elliptic to elliptic to broadly elliptic to obovate-elliptic, 15–159 mm long, 9–75 mm wide, 1.3–2.8 times longer than wide, acute to attenuate at base, acute to acuminate at apex, adaxial surface glabrous or with trichomes along midvein, abaxial surface glabrous or sometimes sparsely pubescent and usually punctate-glandular. Inflorescence spicate; dichasia 3–7(–11) per spike, sessile (rarely borne on peduncles to 1 mm long); flowers sessile; rachis pubescent like younger stems (or with the trichomes denser), usually punctate-glandular. Bracts petiolate or narrowed at base and abruptly expanding into an elliptic to orbiculate lamina, 7–15(–30) mm long, 3.0–10.0(–14.5) mm wide, pubescent like leaves and punctate-glandular on abaxial surface. Bractlets obspatulate (i.e., constricted distally) to hourglass shaped (i.e., with a prominent medial constriction), rarely spatulate (i.e., constricted proximally), (5–)7–15(–20) mm long, equalling or usually longer than calyx, 1–5 mm wide, rounded to acute at apex, abaxial surface pubescent like rachis and punctate-glandular, margin ciliate with flexuose trichomes to 0.5 mm long. Calyx 4.5–9.0 mm long, lobes ovate-elliptic to obovate, rounded to acute to mucronate at apex, abaxial surface puberulent with trichomes 0.05–0.10 mm long and sometimes with ascendant-appressed trichomes to 0.8 mm long along midvein, punctate-glandular, margin ciliate like bractlets (or

FIGURE 8. *Bravaisia berlandieriana* (as *B. tubiflora*) as illustrated by plate 1516 in *Hooker's Icones Plantarum* in 1886. 1, Bud; 2, Pair of stamens; 3, Stamen, anterior side; 4, Stamen, posterior side; 5, Gynoecium; 6, Longitudinal section of ovary; 7, Developing capsule with subtending calyx and bractlets. Magnifications were not provided. Copyright Bentham-Moxon Trustees, used with permission.

the trichomes sometimes denser). Corolla white to pinkish with purplish and yellow markings within, 15–25 mm long, pubescent on external surface of the lobes and upper portions of the throat with dense trichomes 0.2–0.5 mm long; tube 4–8 mm long; throat 6–11 mm long, 6–11 mm in diameter near the midpoint; limb 15–22 mm in diameter with lobes 5–9 mm long. Stamens included in throat or longer pair slightly emergent, shorter pair 7–10 mm long, longer pair 10–14 mm long; thecae 2.5–4.0 mm long including basal awn, pubescent; pollen 56.4–66.2 μm in diameter. Style 14–21 mm long, glabrous. Capsule ovoid to ellipsoid, 6.5–11.0 mm long, glabrous. Seed usually one, subellipsoid, slightly flattened laterally, 3.5–4.3 mm long, 3.0–3.5 mm wide, 1.8–2.6 mm thick, surface glabrous, smooth, shiny (Fig. 8).

PHENOLOGY.—Flowering November through April; fruiting March through May (to July).

DISTRIBUTION.—Northeastern through southeastern Mexico, western Cuba, northern Belize, and northern Guatemala (Fig. 7). The plants occur, often abundantly, on sand dunes (with *Coccothrinax*) along shorelines, beside streams, and in swamps and seasonally marshy areas in regions of coastal scrub, mangrove forest (with *Conocarpus, Rhizophora, Laguncularia,* and *Archosticum*), deciduous and subdeciduous forest, and tropical wet forest at elevations from sea level to 80 m. The plants grow in clayey to sandy, moist to wet soils, some of which are subject to salt water inundation.

Leonard (1951) included *Onychacanthus berlandierianus* in the synonymy of *Bravaisia integerrima.* Examination of the holotype and two isotypes of *O. berlandierianus* reveal Berlandier's early nineteenth-century collection to possess the diagnostic features of what has hitherto been known as *B. tubiflora.* The type collection from the vicinity of Laguna de Tamiahua in northern Veracruz represents the northernmost extent of the distribution of both *B. berlandieriana* and the genus in Mexico. The species has been recollected at Laguna de Tamiahua as recently as 1967. *Bravaisia integerrima* is not known to occur in northeastern Mexico.

The species is easily recognized by its relatively small, pubescent corollas and distinctive bractlets. The bractlets of *B. berlandieriana* usually have a prominent medial constriction and thus appear hourglass shaped. Bractlets that are obspatulate (i.e., constricted distally; e.g., *West 5/2*) can appear similar to those of *B. grandiflora* that have apiculate to caudate apices. At least some bractlets on every specimen of *B. berlandieriana* examined exhibited a prominent medial constriction, however. These two species can be further distinguished by features of the flowers.

Local names noted on herbarium specimens of *B. berlandieriana* are: "chilat" (*Arnason and Lambert 17152*), "hoo-loop" (*Winzerling VIII-14*), "hulaba" (*Gentle 380, 1193*), "hulu" (*Mell 2001*), "hulub" (*Crane 321*), "hulu-bal" (*Stevenson 1*), "hulup" (*Crane 47*), "julub" (*Chan V. 1291*), "julube" (*West 5/2*), "julubo" (*Orozco-Segovia and Gallegos 436*), "kulub" (*Enriquez 398*), and "xulub" (*Vela G. 3046*). Most of these appear to represent variations of a single Mayan name. *Ucan et al. 921* notes the usage of this species as a green dye in Quintana Roo, Mexico. Mendieta and del Amo R. (1981) record the use of poultices made from stems of this species for treatment of mammary abscesses in the Mexican state of Yucatán.

REPRESENTATIVE SPECIMENS EXAMINED.—BELIZE. Belize: Maskall, *Gentle 1193* (A, BM, F, G, GH, K, LL, MICH, MO, NY, US); ca. 12 mi (19 km) W of Belize, *McDaniel 13080* (MO). Corozal: Cerros Maya Ruins, Lowry's Bight, *Crane 47* (LL), *321* (LL); without locality, *Gentle 380* (CAS, F, MICH, US); Freshwater Creek, *Stevenson 1* (F). Orange Walk: Indian Church, *Arnason and Lambert 17152* (MO); without locality, *Winzerling VIII-14* (US). District undetermined: without locality, *Campbell 1* (K), *Stevenson s.n.* (US). CUBA. Pinar del Río: Carabela Grande, *Ruig 3194* (GH, NY, US). Matanzas: Boca de Canasí, *León 13236* (GH), *13679* (US), 14205 (GH, US), *16549* (NY). Province undetermined: without locality, *de la Sagra 679* (P). GUATEMALA. Petén: Dos Lagunas, *Contreras 8369* (US). MEXICO. Campeche: E side of Río San Pedro y San Pablo mouth, *Barlow 17/3* (F, MEXU, WIS); Mpio. Hopelchen, 10–50 km de Xpujil, 18°12′N, 89°26′W, *Chan V. 1291* (F); Canasayab, *Lundell 1414* (GH, MICH, NY); Cd. del Carmen, *Mell 2001* (US); Distr. Champoton, Mokel, *Seler and Seler 4938* (GH); Laguna Atasta, near Isla del Carmen, *West 8/2* (GH, WIS). Quintana Roo: 1 km al S de Akumal, carretera Cancún-Tulum, *Cabrera and Ibarra 1149* (BM, CAS); directly W of Puerto Morelos, *Davidse et al. 20039* (BM, MEXU, MO); Cozumel, *Gaumer 52* (GH); Laguna Guerrero a 20 km N de Chetumal, *Lot and Novelo 799* (GH, MEXU); Cozumel Island, east shore, *Millspaugh 1580* (F); Isla Mujeres, central east coast, *Sauer and Gade 3242* (WIS); 36 km NE de F. Carrillo Puerto, 20 km SW de Vigía Chico, *Tellez and Cabrera 1462* (BM, MEXU); Mpio. Othon P. Blanco, orilla del Río Hondo en Juan Sarabia, 18°30′N, 88°29′W, *Ucan et al. 921* (F). Tabasco: near Playa Azul, ca. 20 km WNW of Paraíso, *Barlow 1/1* (BM, GH, WIS); Balancan, *Mendez et al. 439* (CAS, K, MEXU, MO); Mpio. Centla, a 12 km de Frontera rumbo a La Pera, *Orozco-Segovia and Gallegos 436* (MEXU); Camino Escárcega-Sabankuy, *Vela G. 3046* (ENCB, MEXU); lower Río Naranjeno, Laguna Machona region, *West 5/2* (F, MICH, UC, WIS). Veracruz: Tlacotalpan, *Hahn s.n.* (MO); Laguna Tamiahua, 25

mi (40 km) S of Tampico, *LeSueur 433* (F, GH, TEX); orilla sur del Estero Cucharas cerca de su desembocadura en la Laguna de Tamihahua, *Varquer Y. 23* (MEXU). Yucatán: vicinity of Progreso, *Seler and Seler 3819* (A, F, G, GH, K, US); vicinity of Sisal, *Gaumer et al. 23227 (A, BM, F, G, GH, MO, NY, US); Lake Chichankanab, Gaumer et al. 23662* (F, G, GH, NY, US); Becanchen, *Enriquez 398* (MEXU); Port Silam, *Gaumer 618* (BM, F, MO, US); Chichankanab, *Gaumer 1547* (F), *1872* (A, BM, F, GH, K, MO, NY, US); 4 km E de Celestum, *Lot H. 2603* (GH, MEXU); beach ridge near Chicxulub, *Saunders 93* (ENCB); Mpio. El Cuyo, camino de las Coloradas rumbo al Cuyo, *Ucan and Espejel 788* (F).

Acknowledgments

Funds for field studies were provided by the American Philosophical Society (Research Grant 1572) and the National Science Foundation (BSR-8609852). I am grateful to the curators of the following herbaria for loans and/or allowing me to visit their collections: A, ASU, BM, BR, C, CAS, CGE, DAV, DS, ENCB, F, G, GH, IBUG, K, LE, LL, MEXU, MICH, MO, NO, NY, OXF, P, PH, POM, RSA, TEX, UC, US, W, and WIS. I am indebted to the following persons for their assistance: Frank Almeda (selecting loan), William Anderson (arranging for use of illustration), Bruce Bartholomew (field assistance), Dennis Breedlove (locality assistance), James Doyle (suggestions on pollen interpretation), Vern Durkee and Lucinda McDade (review of manuscript), Charles Michener (insect identification), Susan Middleton (photographic assistance), Wojciech Pulawski (insect identification), Mary Ann Tenorio (SEM operation), Jens Vindum (Danish translation), and Dieter Wasshausen (information on Trichanthereae). I wish to acknowledge the University of Michigan Herbarium and Rogers McVaugh for granting permission to reproduce the drawing of *Bravaisia integerrima,* Timothy Plowman and the Field Museum of Natural History for allowing me to copy and use the plate of *B. grandiflora,* Nancy Morin and the Missouri Botanical Garden for permitting me to reproduce the photograph of *B. integerrima* from Central America, and P. R. Cavalier and the Bentham-Moxon Trustees for permission to reproduce plate 1516 from *Hooker's Icones Plantarum.*

Literature Cited

Bawa, K. S., S. H. Bullock, D. R. Perry, R. E. Coville, and M. H. Grayum. 1985. Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. Amer. J. Bot. 72:346–356.

Bentham, G. 1876. Acanthaceae. Pp. 1060–1122 *in* Genera plantarum, Vol. 2. G. Bentham and J. D. Hooker. Reeve and Co., London.

Blake, S. F. 1917. Descriptions of new spermatophytes, chiefly from the collections of Prof. M. E. Peck in British Honduras. Contr. Gray Herb. 52:59–106.

Bremekamp, C. E. B. 1965. Delimitation and subdivision of the Acanthaceae. Bull. Bot. Surv. India 7:21–30.

Candolle, A. P. de. 1838. Revue sommaire de la famille des Bignoniacées. Biblioth. Universelle Genève 17:117–136.

———. 1845. Bignoniaceae. Pp. 142–248 *in* Prodromus systematis naturalis regni vegetabilis, Vol. 9. A. de Candolle, ed. Fortin, Masson et Sociorum, Paris.

Curran, H. M. 1929. The lands of loba, Colombia. Trop. Woods 19:11–38.

Gibson, D. N. 1974. Acanthaceae. Pp. 328–461 *in* Flora of Guatemala (Fieldiana, Bot. 24 [pt. 10]). P. C. Standley et al., eds. Field Museum of Natural History, Chicago.

Hemsley, W. B. 1886. *Bravaisia tubiflora,* Hemsl. Plate 1516 *in* Hooker's icones plantarum, Vol. 16 (pt. I), ser. 3. J. D. Hooker, ed. Williams and Norgate, London.

Hess, R. W. 1946. Identification of New World timbers. Trop. Woods 86:14–25.

Holmgren, P. K., W. Keuken, and E. K. Schofield. 1981. Index herbariorum. Part 1. The herbaria of the world, 7th ed. Regnum Vegetabile 106:1–452.

Karsten, H. 1865. *Onychacanthus arboreus* Krst. Florae Columbiae 2:111–113.

Lemaire, C. 1847. 12. *Androcentrum* (1) *multiflorum* Ch. L. Fl. Serres Jard. Eur. 3:242 verso.

Leonard, E. C. 1951. The Acanthaceae of Colombia. I. Contr. U.S. Natl. Herb. 31:1–117.

Leonard, E. C. and L. B. Smith. 1964. *Sanchezia* and related American Acanthaceae. Rhodora 66:313–343.

Lindau, G. 1893. Beitrage zur Systematik der Acanthaceen. Bot. Jahrb. Syst. 18:36–64.

———. 1895. Acanthaceae. Pp. 274–354 *in* Die Natürlichen Pflanzenfamilien, Vol. 4 (3b). H. G. A. Engler and K. A. E. Prantl, eds. Wilhelm Engelmann, Leipzig.

———. 1904. Acanthaceae Americanae III. Bull. Herb. Boissier, ser. 2, 4:313–328.

Macbride, J. F. 1934. New or renamed spermatophytes mostly Peruvian. Candollea 5:346–402.

McVaugh, R. 1987. Botanical results of the Sessé & Mociño Expedition (1787–1803). III. The impact of this and other expeditions on contemporary botany in Europe. Contr. Univ. Michigan Herb. 16:155–171.

Meacham, C. A. 1981. A manual method for character compatibility analysis. Taxon 30:591–600.

Mendieta, R. M. and S. del Amo R. 1981. Plantas medicinales del estado de Yucatán. Compania Editorial Continental, Mexico.

Nees von Esenbeck, C. G. 1847. Acanthaceae. Pp. 46–519 *in* Prodromus systematis naturalis regni vegetabilis, Vol. 11. A. de Candolle, ed. Victoris Masson, Paris.

Oersted, A. S. 1854. Mexico og Centralamerikas Acanthaceer. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854:113–181.

Raj, B. 1961. Pollen morphological studies in the Acanthaceae. Grana Palynol. 3:3–108.

Record, S. J. 1929. Trees and shrubs collected by F. C. Englesing in northeastern Nicaragua. Trop. Woods 17:18–38.

Smith, J. D. 1902. Undescribed plants from Guatemala and

other Central American republics. XXIII. Bot. Gaz. (Crawfordsville) 33:249–262.

Sprengel, C. 1825. Systema vegetabilium, Vol. 2. Librariae Dieterichianae, Gottingen.

Stafleu, F. A. and R. S. Cowan. 1979. Taxonomic literature, Vol. II: H–Le, 2nd ed. Bohn, Scheltema and Holkema, Utrecht, etc.

Standley, P. C. 1926. Trees and shrubs of Mexico (Bignoniaceae—Asteraceae). Contr. U.S. Natl. Herb. 23:1313–1721.

Tomlinson, P. B. 1986. The botany of mangroves. Cambridge Univ. Press, Cambridge.

Vasanthy, G. and S. A. J. Pocock. 1986. Radial through rotated symmetry of striate pollen of Acanthaceae. Can. J. Bot. 64:3050–3058.

Wasshausen, D. C. 1970. A synopsis of the genus *Suessenguthia* (Acanthaceae). Rhodora 72:119–125.

Appendix A

Index to Collections Examined

The numbers in parentheses refer to the corresponding species in the text.

Alexander, E. 268 (1), 74-16 (1).
Allen, P. 5714 (1), 7201 (1).
Alston, A. 6057 (1), 6391 (1).
Araquistain, M. and D. Castro 1883 (1).
Arnason and Lambert 17152 (3).
Bailey, L. 606 (1).
Bailey, L. and E. Bailey 1107 (1).
Baker, C. 2363 (1).
Barlow, F. 1/1 (3), 8/2b (3), 17/3 (3).
Bawa, K. 305 (1).
Berlandier, J. 108 (3).
Bernardi, A. 1174 (1), 6311 (1), 6903 (1).
Bernoulli, C. and R. Cario 2042 (1).
Bertero, C. s.n. (1).
Biolley, P. 7105 (1), 7368 (1), 16134 (1).
Borges, F. 9 (1).
Bot. Gard. Herb. 3561 (1).
Bradburn, A. 1476 (3), 1489 (3).
Bradburn, A. and S. Darwin 1230 (3).
Breedlove, D. 49859 (2).
Brenes, A. 6600 (1), 6660a (1), 15137 (1), 20294 (1).
Britton, N. et al. 1099 (1).
Broadway, W. 2555 (1), 7919 (1), s.n. (1).
Bruff, J. 1424 (3).
Bunting, G. 5544 (1), 6197 (1), 6214 (1), 8671 (1), 9150 (1), 10009 (1).
Bunting, G. and L. Licht 740 (1), 1101 (1).
Bunting, G. et al. 13199 (1).
Burger, W. et al. 10601 (1).
Busey, P. 724 (1).
Cabrera, E. and G. Ibarra 1149 (3).
Cabrera, E. et al. 1577 (3), 4589 (3).
Calderón, S. 2138 (1).
Campbell, E. 1 (3).
Carvajal H., S. 742 (1).
Castaneda, R. 34 (1).
Cedillo T., R. 736 (1).
Chalmers, W. s.n. (1).
Chan V., C. 231 (3), 1291 (3), 1302 (3).
Chaves, D. 184 (1).
Chazaro B., M. and A. Dominguez 2158 (1).
Cheesman, E. 140 (1).
Contreras, E. 6694 (2), 6695 (2), 8369 (3), 10563 (2), 11383 (2).
Cooper, G. 25a (1).
Cooper, G. and G. Slater 25 (1), 25a (1), 269 (1).
Covich, A. 6727 (3), 6734 (3).
Crane 47 (3), 321 (3).
Croat, T. 21533 (1), 22538 (1), 21966 (1).
Crueger s.n. (1).
Cuadros V., H. 1491 (1).
Cufodontis, G. 6 (1).
Cumana C., L. 248 (1).
Cuming, H. 1307 (1).
Curran, H. 222 (1), 308 (1), 317 (1).
Daniel, T. 2110 (1), 2144 (1).
Daniel, T. and B. Bartholomew 4882 (1), 4925 (1), 4998 (2).
Darwin, S. and D. White 2214 (3).
Davidse, G. et al. 20039 (3).
Davis, L. and E. Kincaid 55-7 (1).
Delgado, E. 349 (1).
Detling, L. 8801 (1).
Diguet, L. s.n. (1).
Dodge, C. and W. Thomas 6393 (1).
Dugand, A. 13 (1), 83 (1), 168 (1), 412 (1), 542 (1), 580 (1).
Dugand, A. and H. Garcia B. 2324 (1).
Dugand, A. and R. Jaramillo 4094 (1).
Dunlap, V. 23 (1).
Duran, R. and I. Olmsted 832 (3), 853 (3).
Elias 444 (1), 487 (1), 952 (1), 974 (1), 1265 (1), 1507 (1).
Englesing, F. 147 (1).
Enriquez 398 (3).
Fendler, A. 2041 (1).
Flores 8096 (3).
Fontiveros, R. 17 (1).
Forero, E. and R. Jaramillo 500 (1).
Funcke, N. and L. Schlim 441 (1).
Galeotti, H. 510M (1).
Garnier, A. 1003 (1).
Gaumer, G. 52 (3), 618 (3), 1547 (3), 1872 (3), 1873 (3).
Gaumer, G. et al. 23227 (3), 23650 (3), 23662 (3).
Gentle, P. 380 (3), 1193 (3), 4555 (2).
Gentry. A. 524 (1).
Gentry, A. and G. Morillo 10325 (1).
Goldman, E. 600 (3).
Gómez-Pompa, A. 711 (1), 1299 (3).
González M., F. and J. Villaseñor R. 11947 (1).
González Q., L. 3496 (1).
González T., A. 46 (1).
Haber 438 (1).
Haenke, T. 1439 (1).
Hahn, M. s.n. (3).
Hartshorn, G. 1172 (1), 1294 (1).
Haught, O. 3989 (1).
Hazlett, D. 1189 (1).
Hernández, H. s.n. (1).
Hernández, M. s.n. (1).
Hughes, C. and B. Styles 73 (1).
Jiménez, A. 505 (1).
Jiménez L., O. 367 (1).
Jiménez M., A. 301 (1), 1702 (1), 1710 (1).
John, A. 335 (1).
Johnson 187 (2).
Johnson, E. s.n. (1).
Jurgensen, C. 96 (1).

Lamb, A. 58 (2).
Langlassé, E. 831 (1).
Lehmann, F. s.n. (1).
León 13236 (3), 13679 (3), 14205 (3), 16549 (3).
LeSueur, H. 433 (3).
Lewis, W. et al. 886 (1).
Liesner, R. 4847 (1), 4982 (1).
Linden, J. 441 (1).
López-Palacios, S. 1810 (1).
Lot H. 2603 (3).
Lot and Novelo 799 (3).
Lundell, C. 1414 (3).
Lundell, C. and A. Lundell 8146 (3).
Magaña, M. and S. Zamudio 128 (1).
M.A.M.A. 677 (1).
Marshall, R. 12474 (1).
Matuda, E. 16218 (1), 38307 (3).
McDaniel, S. 13080 (3).
McVaugh, R. 15578 (1), 22884 (1), 23009 (1).
Mell, C. 2001 (3).
Mendez, F. et al. 439 (3).
Millspaugh, C. 206 (3), 1580 (3).
Miranda, F. 398 (3), 4325 (1), 8082 (3).
Molina R., A. 2130 (1).
Molina R., A. et al. 17645 (1).
Moreno, P. 496 (3), 562 (3), 6595 (1).
Mori, S. et al. 14565 (1).
Nelson, E. 2375 (1), 7001 (1).
Oersted, A. 10624 (1), 10633 (1), 10634 (1), s.n. (1).
Otto, E. 538 (1).
Orozco-Segovia, A. and E. Gallegos 436 (3).
Peck, M. 730 (2).
Pennell, F. 4697 (1).
Penner, J. s.n. (3).
Pennington, T. and J. Sarukhan K. 9354 (1), 9491 (1), 9522 (1), 9606 (1).
Pittier, H. 5807 (1), 7727 (1), 7760 (1), 11449 (1), 13358 (1).
Puga, M. 2916 (1).
Pursell, R. et al. 8446 (1), 8524 (1).
Quero, H. and R. Grether 2677 (3).
Ramirez V., G. 19 (1).
Ramos M., F. 38307 (3).
Romero, R. 34 (1), 980 (1).
Ruig 3194 (3).
Rzedowski, J. 15397 (1), 31811 (1).
Sagra, de la 679 (3).
Sauer, J. and Gade 3208 (3), 3242 (3).
Saunders, G. 93 (3).
Schipp, W. 1259 (2).
Schott 302 (3).
Schubert and A. Gómez-Pompa 1607 (3).
Seler, E. and C. Seler 1609 (1), 3819 (3), 4938 (3).
Sessé, M., J. Mociño, et al. 275 (1), 2147 (1), s.n. (1).
Shannon, W. 5005 (1).
Smith, F. 123 (1), 270 (1).
Smith, H. 1869 (1).
Soto, J. and A. Ramón de Soto 759 (1).
Soto, J. and R. Torres C. 2714 (1).
Standley, P. and J. Valerio 45073 (1), 45099 (1).
Stevenson, D. 1 (3), s.n. (3).
Steyermark, J. 45031 (2), 55551 (1), 61181 (1), 62161 (1), 89202 (1).
Steyermark, J. and V. Carreño E. 106903 (1).
Steyermark, J. et al. 121317 (1), 123017 (1).
Stone 287 (3).
Stork, H. 23b (1).
Tate, R. 309 (1).
Tejera, E. 113 (1).
Tellez, O. and E. Cabrera 1462 (3), 1508 (3).
Tellez, O. et al. 4310 (1).
Tonduz, A. 13884 (1).
Tucker, J. 864 (1).
Tuerckheim, H. von 7924 (2), 8259 (2).
Tún Ortíz, R. 1642 (2), 2351 (2).
Ucan, E. and I. Espejel 788 (3).
Ucan, E. and J. Flores 1036 (3).
Ucan, E. et al. 921 (3).
Utley, J. and K. Utley 3987 (1).
Vargas s.n. (1).
Varquer, Y. 23 (3).
Vela G., L. 3046 (3).
Ventura A., F. 19954 (1), 20001 (2).
Villegas, M. 247 (1).
Villers, L. 21 (3).
Vogl, P. 1387 (1).
Watson, S. 240 (2).
Wendt, T. et al. 3114 (1), 4076 (1).
West, R. 5/2 (3), 8/2 (3).
Whiteford, C. 3219 (2).
Williams, L. 12341 (1), 12904 (1).
Williams, L. O. 8913 (1).
Williams, L. O. and T. Williams 24486 (1).
Williams, L. O. et al. 25070 (1).
Winzerling VIII-14 (3).
Wright, C. s.n. (1).
Wurdack, J. and J. Monachino 39712 (1).

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 9, pp. 133–254, 17 figs., 1 table, 35 plates February 5, 1988

DIATOMS (BACILLARIOPHYCEAE) FROM SURFACE SEDIMENTS IN THE SAN FRANCISCO BAY ESTUARY

By

Richard A. Laws

Department of Earth Sciences, University of North Carolina at Wilmington, Wilmington, North Carolina 28403

ABSTRACT: Two hundred seventy-three diatom species were identified from sediments in the San Francisco Bay estuary. The most common species in surface sediment samples are *Thalassiosira decipiens, Paralia sulcata, Nitzschia acuminata, Ditylum brightwellii,* and *Cyclotella striata,* whereas the most diverse genera are *Navicula* (26 species), *Nitzschia* (25), *Fragilaria* (13), *Achnanthes* (11), and *Cocconeis* (9). Descriptive multivariate analyses of species frequency data from 51 surface sediment samples extracted seven Q-mode clusters and five principal components for the 50 most abundant species. Significant patterns of diatom abundance and distribution in surface sediments of the estuary include: (1) highest diatom abundance occurs in the shallow subtidal to intertidal areas, especially in Suisun Bay and northern San Francisco Bay (Albany mud flats); (2) areas of high diatom abundance in sediment samples correspond to areas of high microalgal biomass measured as chlorophyll-a and phaeophytin; (3) areas of high species diversity (richness) in San Pablo Bay and southern San Francisco Bay do not correspond to areas of high abundance; (4) the dominant species in the estuary based on sediment analysis are benthic or meroplanktonic; (5) the distribution of species assemblages, as determined by Q-mode cluster and R-mode principal components analyses, follows gradients of salinity and depth; (6) the ratio of *Paralia sulcata* to *Thalassiosira decipiens* varies directly with salinity and may serve as a salinity indicator in ancient sediments.

Submitted 15 July 1985. Accepted 28 January 1986.

INTRODUCTION

San Francisco Bay (Fig. 1) is the largest estuary in the western United States and is an outstanding, albeit large and complex, natural laboratory for the study of estuarine diatoms. It has been estimated that over 500 species may inhabit the San Francisco Bay system (pers. comm., R. L. J. Wong and A. D. Mahood 1980), and Wong and Cloern (1981) listed 105 species of diatoms from the plankton alone. Furthermore, the bay system includes a wide variety of habitats such as salt- and freshwater marshes, intertidal creeks that range from fresh water at low tide to highly brackish at high tide, subtidal brackish water tidal creeks, extensive intertidal and subtidal mud flats, and channels to depths of 20 m. Yet, despite the bay's obvious commercial and esthetic importance, its varied habitats, and rich diatom flora, no illustrated systematic catalog of the diatoms in the bay exists.

The purpose of this report is to describe the taxonomic composition and distribution of diatoms from sediments in the San Francisco Bay system. Taxonomic data are based on examination of cleaned surface-sediment samples, and distributional studies are based on multivariate

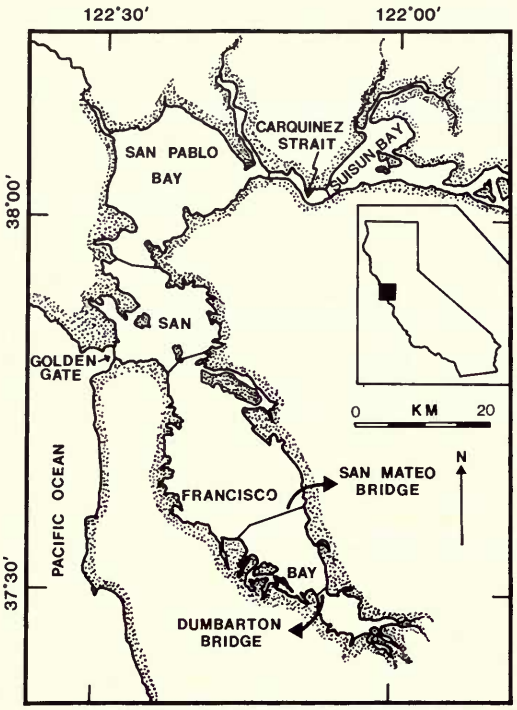


FIGURE 1. Location of study area.

analyses of relative species frequencies. The floral list and distributional data are no doubt incomplete, a result of the nature of the sampling and the immensity of the problem. However, I believe that this study presents a majority of the common species in the bay and portrays the significant large-scale distributional patterns of those species. Such data should be useful to researchers and governmental agencies currently studying the bay, and these data will provide a basis for comparison in future studies of diatoms in the bay.

Previous studies of diatoms in San Francisco Bay were directed largely toward the phytoplankton. Storrs et al. (1966) provided the first detailed systematic survey of phytoplankton in the bay. That report described seasonal variation in phytoplankton abundance along a transect from Suisun Bay to the Golden Gate. They recorded a summer phytoplankton maximum in Suisun Bay and a spring maximum in other areas. Subsequent studies (Peterson et al. 1975; Arthur and Ball 1979; Ball and Arthur 1979; Conomos 1979; Peterson 1979) supported those findings. Sitts and Knight (1979) described the daily, seasonal, and vertical changes in phytoplankton from a single station at the eastern end of Suisun Bay. They reported a maximum abundance from February to May and also noted diel changes in composition and abundance at that station. Cloern (1979) summarized current information on phytoplankton dynamics in the bay. Wong (1975) reported phytoplankton species composition from three stations in the central bay near the Golden Gate. Mahood et al. (1986) in a comprehensive study of *Thalassiosira* recognized 23 species largely from plankton samples taken in Suisun Bay.

Studies of the benthic diatoms in the bay are few. Wong (1982) described seasonal changes in species composition in sediment samples from a single station in Suisun Bay. Thompson and Laws (1982) discussed seasonal changes in productivity and species composition of the microphytobenthos through a yearly cycle.

Atwater et al. (1977), Wagner (1978), Sloan (1981), and Laws (1982, 1983*b*) reported diatoms from borehole samples of late Pleistocene estuarine deposits preserved beneath the present bay. Atwater et al. (1977) distinguished between centrics and pennates and discussed their relative abundance. Wagner (1978) recognized 27 species of diatoms in the sand-sized fraction of sediments from two cores in the central area of the bay. Sloan (1981) recorded 16 taxa in the sand-sized portion of sediments from a series of boreholes which span the southern bay. Laws (1982, 1983*b*) discussed the composition and distribution of diatoms in the silt-clay fraction of samples from the same series of boreholes in the southern bay.

The physiography, hydrodynamics, physical and chemical properties, biota, and geological history of San Francisco Bay estuary are summarized by Conomos (1979).

Materials and Methods

Samples were obtained in conjunction with studies of San Francisco Bay estuary by the U.S. Geological Survey, Bay and Estuarine Study Group (Menlo Park). Concurrent studies of the biochemical and physical aspects of the sediment samples by that group greatly facilitated this work (see Thompson et al. 1981).

Surface sediment samples were collected from the U.S. Geological Survey research vessel ESTERO, a shallow-draft boat capable of maintaining station in depths as shallow as one meter.

Forty-seven stations throughout the estuary (Fig. 2–7) were sampled over a 4-day period on 26 February and 6, 7, and 13 March 1980. Measurements of salinity, temperature, depth, and turbidity of the water column were taken at each station (see Thompson et al. 1981). Shipboard equipment used to measure these parameters is described by Thompson et al. (1981).

Thompson et al. (1981) used a gravity corer to collect simultaneously ten replicate samples of undisturbed surface sediment at each station in polycarbonate core barrels having a 9.6 mm inner diameter. One of the cores was analyzed for diatoms. The others were analyzed for chlorophyll-a, phaeopigments, and grain size (Thompson et al. 1981). Four additional stations were sampled by hand at low tide, using the same core barrels in the Albany salt marsh and mud flats (Fig. 5) on 18 January 1981. Fifty-one stations were sampled for surface sediment.

The upper 1 cm (0.72 cc) of each surface sediment core sample was extruded and washed according to the procedures modified after Setty (1966) and Schrader and Gersonde (1978) (see Laws 1983*b*). Strewn slides of the washed material were prepared and diatom species enumerated according to the techniques discussed in Laws (1983*a*). The number of valves counted per sample varies from 265 to 888 (see Table 1) with a mean of 558 valves per sample. Ninety-two percent of the samples comprise 450 or more valves. Sample size of 400–500 valves is commonly used in similar studies of benthic diatoms or diatoms in sediment samples (e.g., McIntire and Overton 1971; Main and McIntire 1974; Amspoker and McIntire 1978; McIntire 1978; Schrader 1978; Schrader and Gersonde 1978; Schuette and Schrader 1979, 1981; Colijn and Dijkema 1981; Sullivan 1982) and was justified by McIntire and Overton (1971), Schrader and Gersonde (1978), and Laws (1983*a*).

Additional subsurface samples from a late Pleistocene (Sangamon) unit, here informally designated the Yerba Buena mud, were examined. The Yerba Buena mud occurs in the subsurface beneath southern San Francisco Bay (Sloan 1981). Data from the Yerba Buena mud are included in the floral list for comparative taxonomic purposes and completeness. Those samples come from boreholes along the proposed Southern Crossing (Fig. 1) which were drilled in 1969 by the California Department of Transportation Division of Bay Toll Crossings under contract TC 82-032. Samples retained from those boreholes are archived at the U.S. Geological Survey which kindly provided the samples for this study. The original borehole samples, each approximately 1 m long, are divided into three parts and stored in jars. The jar samples, each 5 cm in diameter and up to 15 cm in length, were split lengthwise along the diameter and sampled using the same polycarbonate core barrels as above. Sloan (1981) and Laws (1983*b*) discussed the microfauna, microflora, and stratigraphy of the Yerba Buena muds in detail.

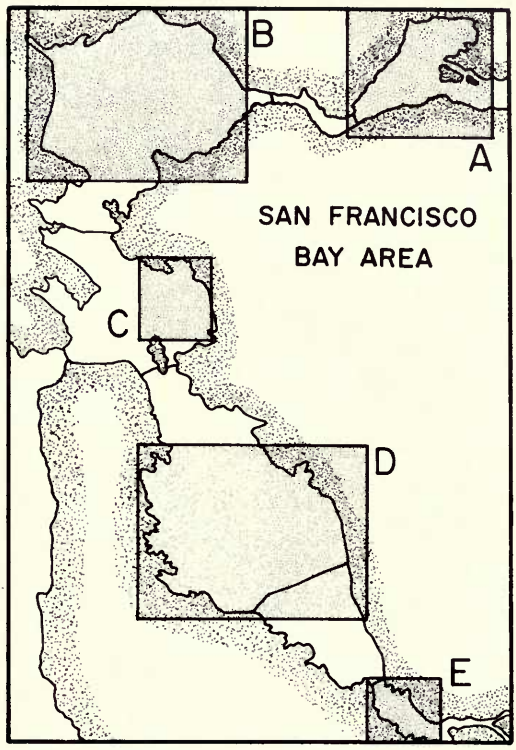


FIGURE 2. Index for Figures 3–7 and 9–13. A = Figures 3 and 9, B = Figures 4 and 10, C = Figures 5 and 11, D = Figures 6 and 12, E = Figures 7 and 13.

Data Analysis

Raw data consist of species enumerations (frequencies) from each of the 51 surface-sediment samples. These raw data were standardized by percent transformations to relative frequency data and subjected to Q-mode cluster and R-mode principal components analyses. Throughout the discussion of these analyses diatom species constitute the mathematical "variables" from each

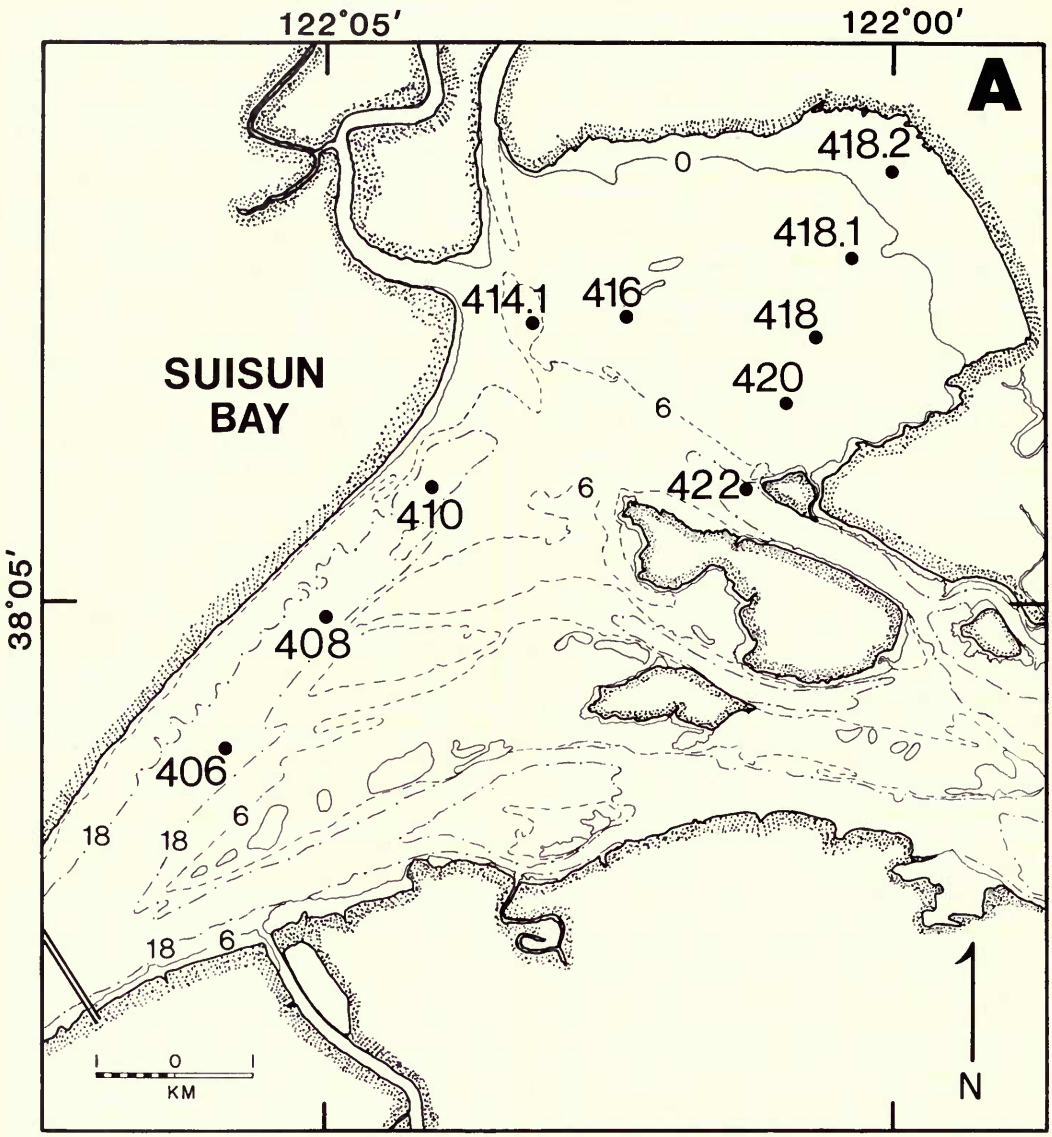


FIGURE 3. Location of sampling stations in Suisun Bay. Bathymetry in feet at mean lower low water.

sampling station. Therefore, the terms "species" and "variables" are used interchangeably.

Those two multivariate statistical analyses require the basic assumption that the data represent random samples of the original populations. The validity of that assumption hinges on consideration of taphonomic bias, sampling and preparation techniques, and counting techniques. The methods used in this study, discussed in Laws (1983*a, b*), were carefully designed to minimize those biases.

The Q-mode cluster and R-mode Principal components analyses are mathematically independent and were performed separately. However, each yields similar types of results that can be used to test the results of the other procedure, a method not unlike reciprocal illumination. Both analyses were performed on a matrix consisting of the 50 most abundant species distributed over the 51 sampling stations (i.e., a 50 × 51 data matrix).

The analyses were performed by the Biomed-

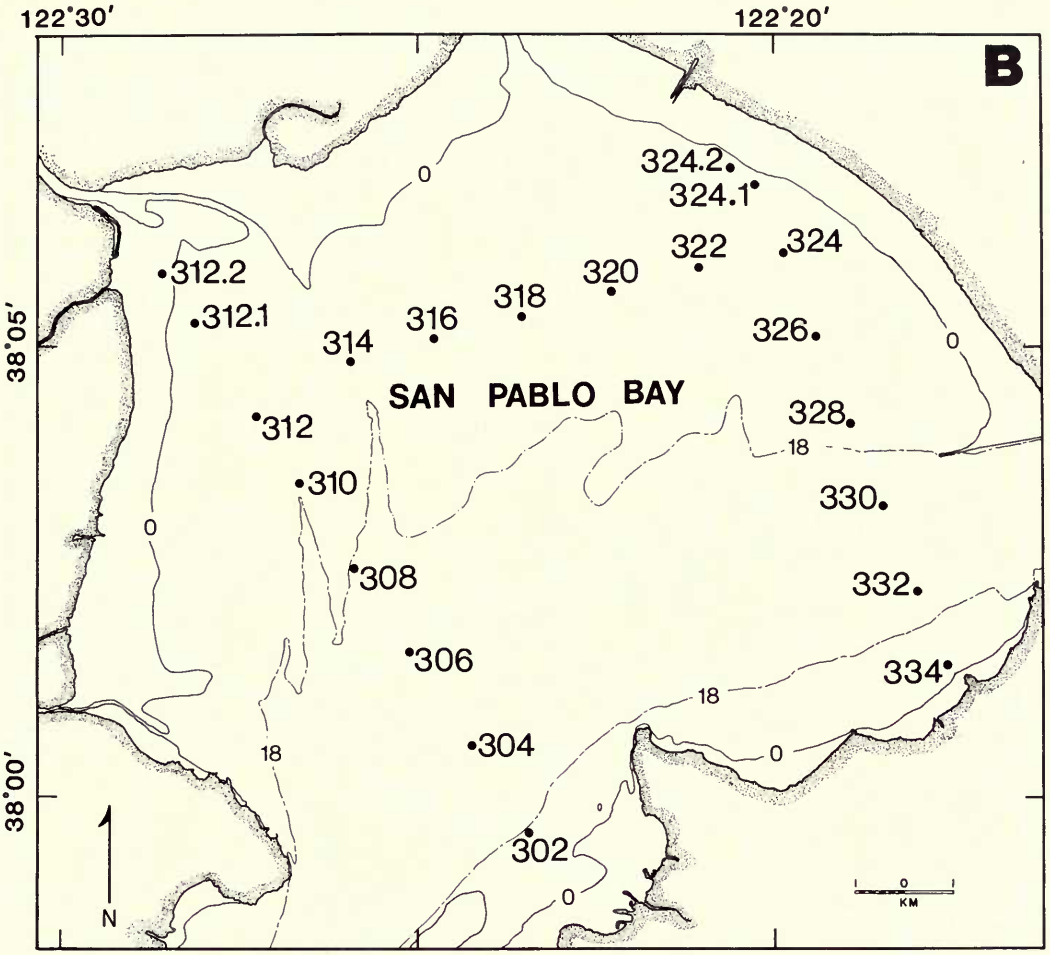


FIGURE 4. Location of sampling stations in San Pablo Bay. Bathymetry in feet at mean lower low water.

ical Computer Programs P-series (BMDP), programs P2M, Q-mode cluster analysis (revised 7/7/75), and P4M, principal components analysis (revised 7/7/75) (Dixon 1981). These programs were developed by the University of California at Los Angeles, Biomedical Computer Facility with the aid of a grant from the National Institutes of Health.

Q-mode cluster analysis groups localities on the basis of similarity of species content using a chi-square measure of similarity (or distance) between samples. The distance coefficient, d (or chi-square value) for the i variables in the jth and lth samples is written

$$d_{jl} = \left\{ \sum_i [(x_{ij} - e_{ij})^2/e_{ij} + (x_{ij} - e_{il})^2/e_{il}] \right\}^{1/2}$$

where

$$e_{ij} = (x_{ij} + x_{il}) \sum_i x_{ij}/N_{jl}$$

and

$$N_{jl} = \sum_i (x_{ij} + x_{il}).$$

Simply stated, this distance measure is the chi-square value comparing the two samples j and l for each variable summed over all variables. The parameters e_{ij} and e_{il} serve as estimates for the mean (or expected) value of each variable based on the total for all variables in the two samples.

Once these distance measures are calculated,

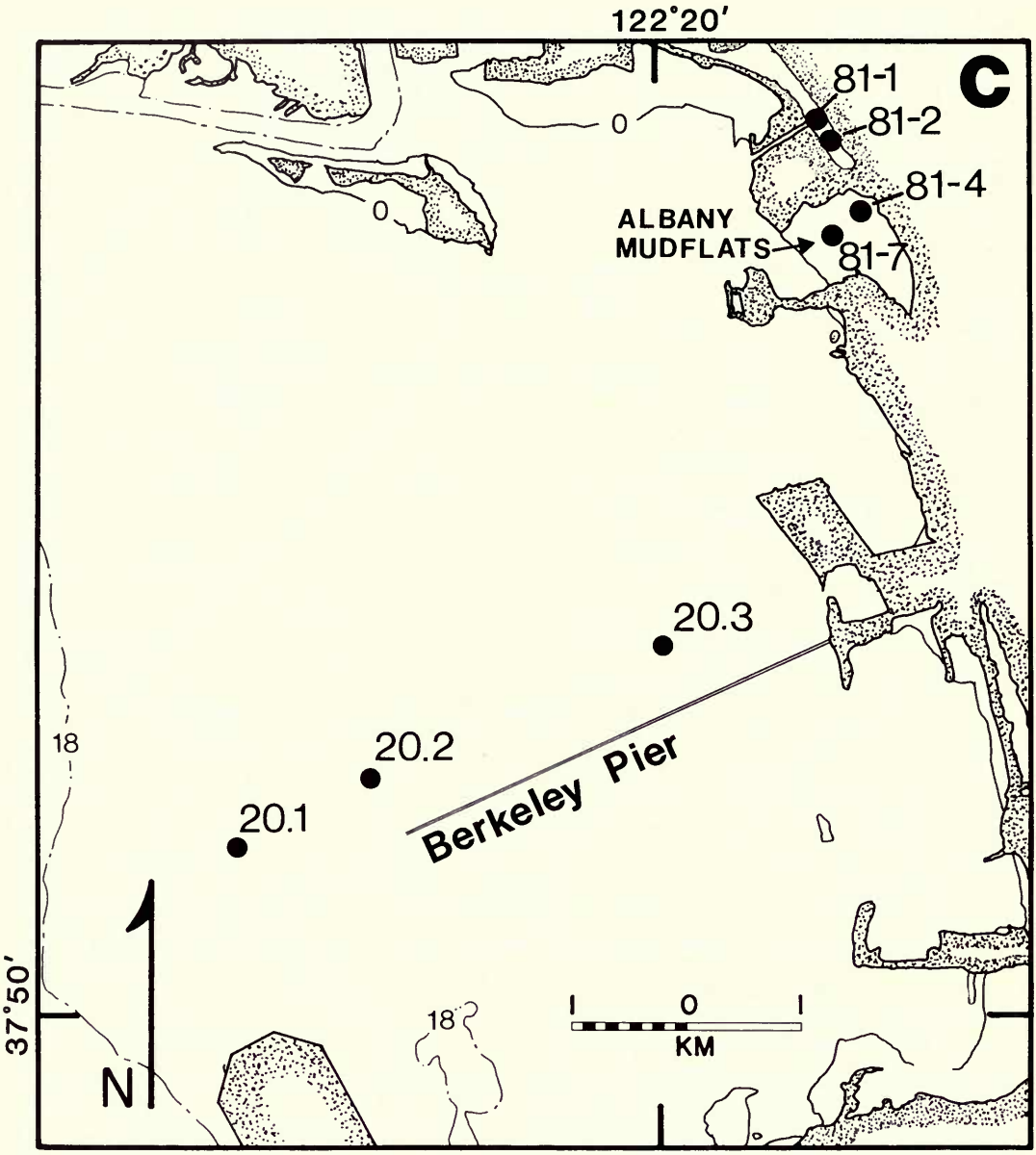


FIGURE 5. Location of sampling stations in northern San Francisco Bay and Albany mud flats. Bathymetry in feet at mean lower low water.

the samples are clustered (amalgamated) by the weighted average linkage method which calculates an arithmetic average distance between clusters and a potential new member. Sneath and Sokal (1973) gave a detailed discussion of this procedure.

Placement of boundaries between clusters (i.e., choice of a discrete value of the distance coefficient between clusters) is subjective but is based on two criteria: (1) the clusters should be logically consistent with other independent data (e.g., geography, environment), and (2) by comparing the real data clusters to clusters of random numbers for a similar-sized matrix. The second method gives an upper limit for an amalgamation distance coefficient that is as likely due to random

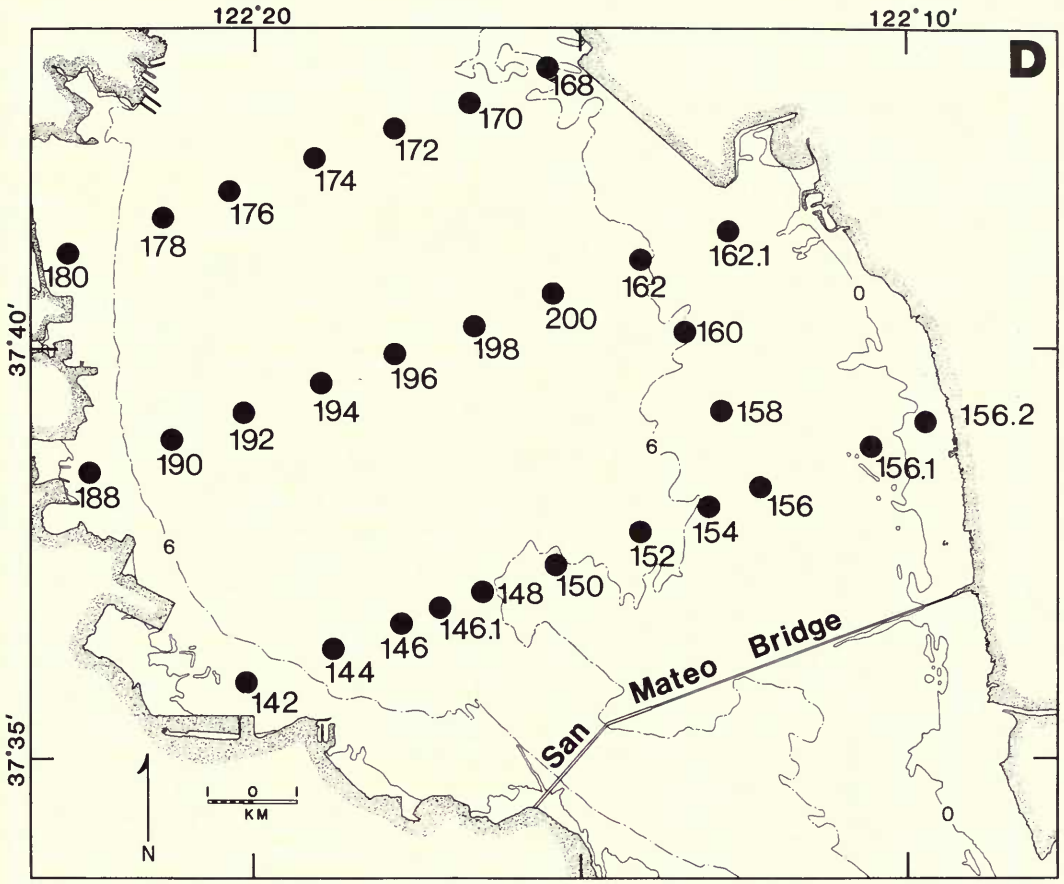


FIGURE 6. Location of sampling stations in southern San Francisco Bay north of the San Mateo Bridge. Bathymetry in feet at mean lower low water.

effects as to real correlation (see Harper 1978). Once cluster boundaries have been established, clusters are plotted against the original pattern of sample distribution.

R-mode principal components analysis with a Varimax rotation was performed on the matrix of species frequencies. Details of the methods of data analysis and interpretation used in this study are given in Frane and Hill (1976), Morrison (1976), Neff and Marcus (1980), and Laws (1983*a*). Briefly, principal components analysis evaluates the correlations among variables in large data sets by projecting the variables onto components (axes) drawn through variable hyperspace so that the dominant variables in each component are highly correlated with each other, but not with variables in other components. The interpretation of each component is based on the proportionate correlation (loading) of each variable to each component. Each sample then receives a score for each component. The scores represent the proportionate contribution of each component to the variance in each sample. In other words, the analysis extracts groups of highly correlated species and determines the proportionate contribution of each species group to the total species assemblage in each sample. In this way, the analysis identifies recurrent groups of dominant species and enables one to map the distribution of these species associations relative to the original sample locations.

A successful analysis requires the proviso that each variable be rather highly correlated with some other variables but not all others. Principal components analysis, as used here, is an exploratory and descriptive method and is not used for hypothesis testing. As such it requires no other computational or statistical assumptions.

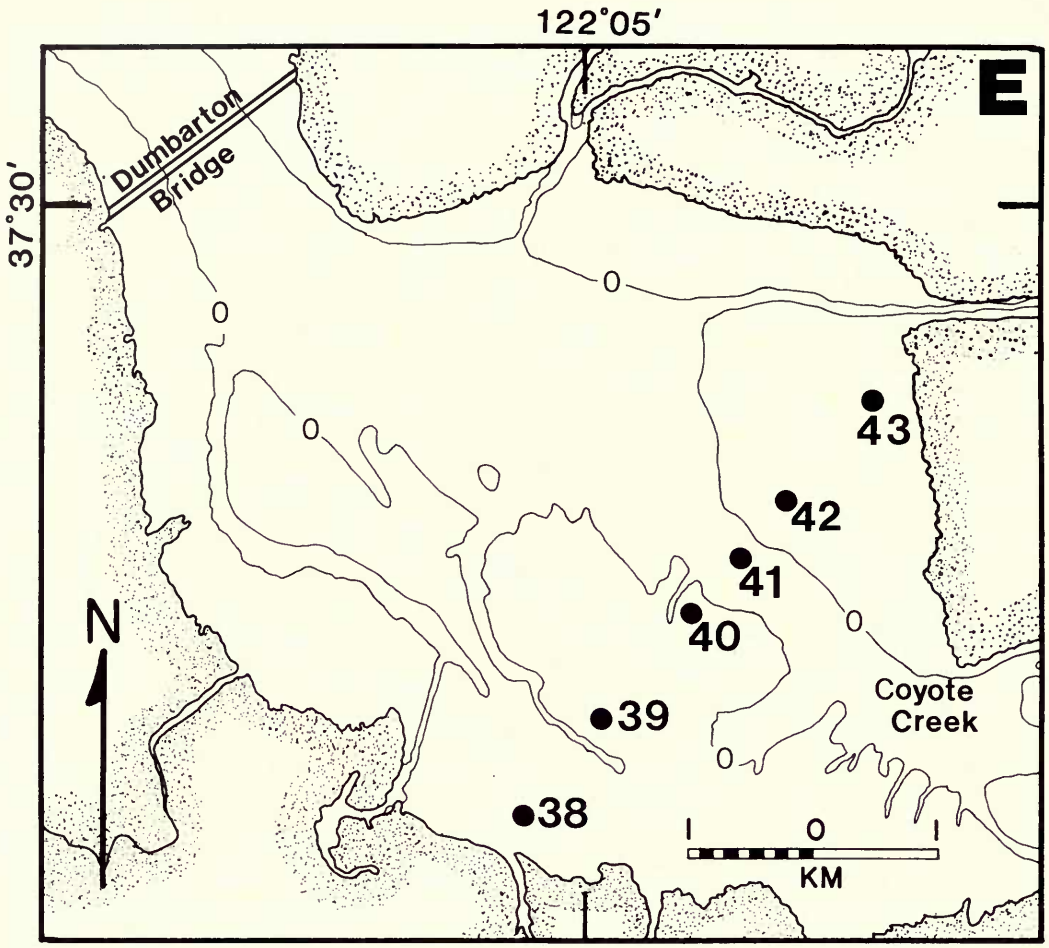


FIGURE 7. Location of sampling stations in southern San Francisco Bay south of the Dumbarton Bridge. Bathymetry in feet at mean lower low water.

Principal components were extracted from the covariance matrix because it more precisely expresses the variation in the data set when variables are correlated. The initial components extracted from the data set are orthogonal and by definition are independent or uncorrelated. The initial components are rotated using the so-called Varimax rotation to yield a more interesting configuration; that is, so that each variable is highly correlated with a small number of components. That rotation maintains the orthogonality of the components and seems appropriate because one objective is to find independent clusters of variables and samples so that distributional patterns are more easily interpreted.

It is possible to generate as many initial components as variables, but a successful analysis must yield some number of major (principal) components that is considerably less. Major components were identified as those components that explained 90% of the total variance in the data set, were consistent with other independent data, and did not duplicate information in other major components. The major components are interpreted according to their constituent species. This is accomplished by plotting the loadings for a selected set of species for each major component (see Fig. 15). The selected species are those that have a relatively high loading on at least one of the major components. The major components are typically considered as summary variables and may be interpreted as indicators of some underlying environmental parameters. Therefore, a few large scores for each sample

replace the values of many original variables. The analysis, thereby, summarizes the information in a large data set into a few major components without loosing significant information.

Results

Diatom Flora

I counted a total of 28,460 valves from 51 surface-sediment samples for an average of 558 valves per sample. In addition, I examined approximately 37,000 valves from 64 samples of the Yerba Buena muds (for a summary of species enumerations for surface-sediment samples, see Table 1). Complete data for species frequencies are given in Laws (1983*b*). Counts ranged from 265 to 888 valves per sample. Diatom frequency ranged from 27 to 3,700, and it was highest in the Albany mud flats area and in Suisun Bay. (Diatom frequency is a relative measure of abundance based on number of valves per standard area on a slide. Its measurement and significance is discussed in Laws [1983a]). As expected, high diatom frequency correlates with high values of chlorophyll-a and phaeopigments as reported by Thompson et al. (1981).

Two hundred thirty-two species and varieties from 59 genera were recognized from surface-sediment samples. Forty-one species are restricted to the Yerba Buena muds. The complete floral list appears below. The five most abundant species are *Thalassiosira decipiens, Paralia sulcata, Nitzschia acuminata, Ditylum brightwellii,* and *Cyclotella striata,* whereas the five most speciose genera are *Navicula* (26 species), *Nitzschia* (25), *Fragilaria* (13), *Achnanthes* (11), and *Cocconeis* (9). The number of species per sample ranged from 24 to 73. High diversity (i.e., species richness; R, Table 1) occurs in San Pablo Bay and southern San Francisco Bay (compare Table 1 and Fig. 2–7).

The abundance and diversity data suggest several patterns. Areas of high abundance typically occur in nearshore intertidal marshes and mud flats protected from the direct effects of strong winds and currents. These areas of high abundance are not necessarily areas of high species richness. Samples with high abundance (diatom frequency) are typically dominated by a single species and often show low species richness. Colijn and Dijkema (1981) described similar patterns from intertidal areas of the Wadden Sea.

Table 1. Summary of Diatom Species Enumerations from Surface Sediment Samples in San Francisco Bay Estuary. N = number of valves; T = number of transects across the slide; DF = diatom frequency (N/T); R = number of species.

Station	N	T	DF	R
38	462	8	58	55
39	470	7	67	47
40	465	4	116	37
41	265	10	27	29
42	526	4	132	39
43	547	3	182	47
20.1	518	10	52	60
20.2	581	10	58	58
20.3	367	10	37	53
200	489	10	49	50
192	754	2	377	42
190	614	7	88	67
188	572	5	114	62
180	490	2	245	45
178	564	6	94	61
174	544	8	68	62
172	450	10	45	59
162.1	557	6	93	52
156.1	554	4	139	50
156.2	556	10	57	56
152	524	2.5	210	41
148	526	6	88	49
146.1	491	6	82	51
144	462	10	46	48
142	564	5	113	48
334	354	10	35	47
332	424	10	42	56
330	574	5	115	60
328	490	5	98	53
326	567	6	95	67
324	505	6	84	61
324.1	573	9	64	61
318	485	8	61	58
312	571	10	57	68
312.1	554	10	55	73
312.2	628	8.5	74	71
310	533	8	67	61
308	568	7	81	63
306	620	4	155	59
406	651	0.36	1,808	49
410	643	1	643	49
414.1	876	0.80	1,095	43
416	473	1	473	41
418	670	0.42	1,595	43
418.1	682	0.44	1,550	33
418.2	687	0.24	2,863	24
422	888	1	888	55
81-1	588	0.16	3,675	30
81-2	701	0.71	987	44
81-4	575	1.50	383	38
81-7	668	1	668	44

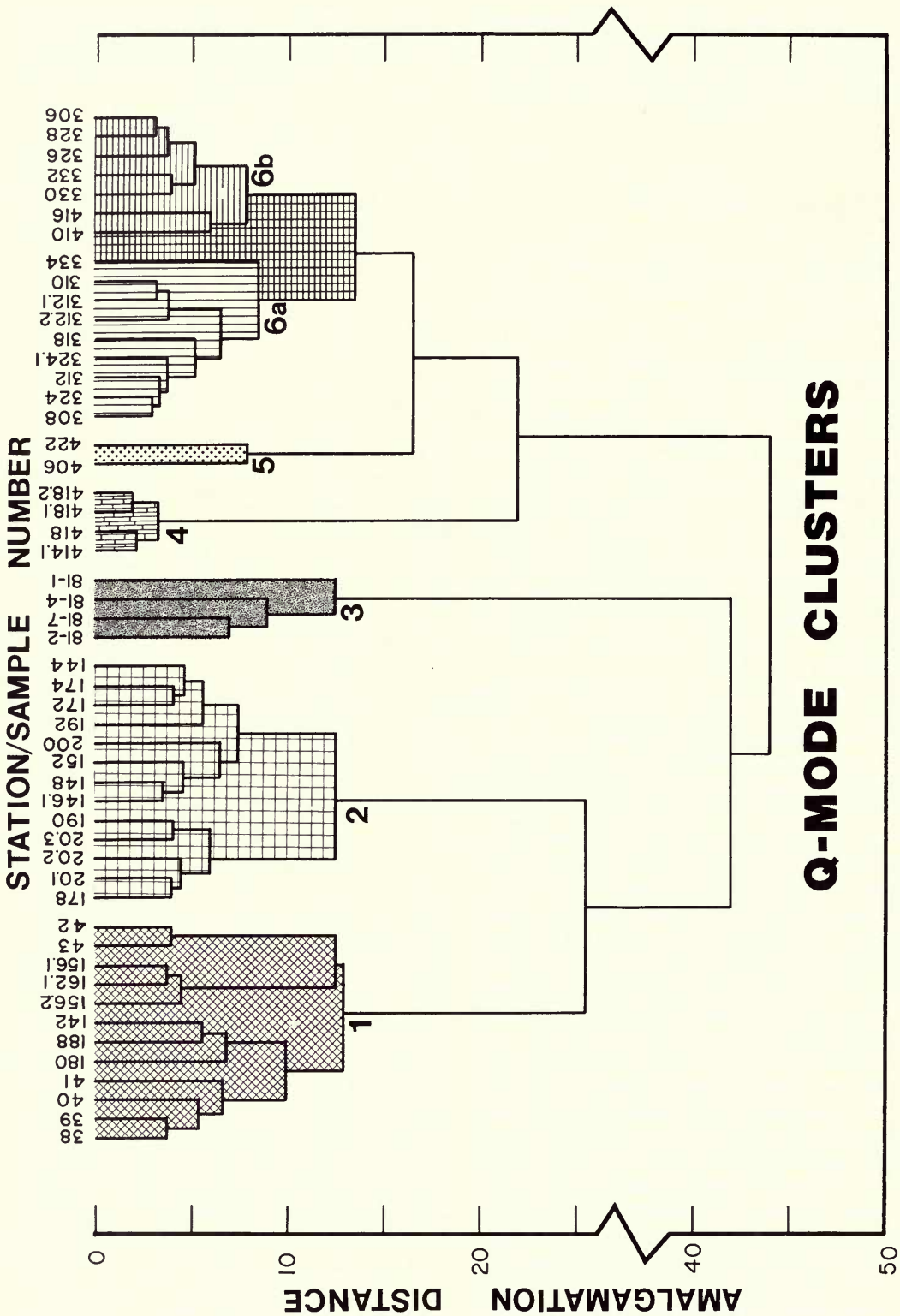


FIGURE 8. Q-mode clusters of 51 of the stations shown in Figures 3–7.

They correlated these patterns with immersion time, photoperiod, and sediment type.

High abundance in Suisun Bay is attributable to its location within the null or entrapment zone of the estuarine circulation (Arthur and Ball 1979; Cloern 1979; Wong and Cloern 1981). The dominance of a single species, *Thalassiosira decipiens,* in that area is unexplained, but it is probably related to its particular tolerance for the conditions in that area.

The cause for high abundance in the Albany salt-marsh and mud-flat samples is not so obvious and may be related more to biotic interactions than to physical constraints. Diversity is low in these samples relative to the data set as a whole, but no one species dominates as in Suisun Bay. Protected salt marshes and mud flats such as in Albany are areas where large quantities of fine-grained sediment and organic debris accumulate (Atwater et al. 1977; Atwater 1979). High nutrient levels might be maintained by accelerated bacterial activity in such areas. Furthermore, a variety of epiphytic and epipelic habitats distributed along gradients of salinity, exposure time, insolation, and sediment size may contribute to high productivity.

Q-mode Cluster Analysis

Q-mode cluster analysis based on frequency data for the 50 most abundant taxa defined seven clusters of samples (Fig. 8). Those clusters form discrete, geographically coherent units when plotted against station locations (Fig. 9–14). That distributional pattern follows closely the distribution of salinity and depth in the Bay system (compare Fig. 3–7 and 9–14). Cluster 1 is restricted to the margin and shallow areas of southern San Francisco Bay. Cluster 2 plots in the deeper central portions of San Francisco Bay. The boundary between clusters 1 and 2 follows closely the 6-ft (1.83 m) isobath throughout southern San Francisco Bay. Cluster 3 includes the four stations in the Albany mud flats and salt marshes. Cluster 4 is restricted to the northern parts of Suisun Bay at depths shallower than 6 ft (1.83 m). Cluster 5 includes only two stations that are in the deeper channels of Suisun Bay. Cluster 6a groups those stations in the northwestern and southeastern parts of San Pablo Bay in water shallower than 6 ft (1.83 m). Cluster 6b represents stations in the deeper channels (6 ft [1.83 m] or more) of San Pablo and Suisun Bays. Clusters 6a and 6b are labeled to reflect their similar species content but are treated separately because of their discrete distributional patterns.

Epipelic and epiphytic taxa including *Nitzschia acuminata, N. pusilla, Cocconeis vitrea, Gyrosigma fasciola,* and *Navicula tripunctata* dominate stations in cluster 1. These species are typical of brackish and marine coastal environments. Stations in cluster 2 have high frequencies of the marine-to-brackish-water planktonic species *Paralia sulcata, Ditylum brightwellii, Actinoptychus senarius,* and *Cyclotella striata/stylorum.* Numerous epiphytic and epipelagic species are present at stations in cluster 3, but *Nitzschia sigmaformis* and *Achnanthes haukiana* are dominant. Other common species include *Navicula tripunctata, N.* spp., *Gyrosigma fasciola, Melosira moniliformis, M. numuloides,* and *Nitzschia* spp. *Thalassiosira decipiens* overwhelmingly dominates cluster 4. Some confusion exists over the life habits of this species, which is probably benthic in fresh to moderately brackish water (G. Fryxell, pers. commu. 1982). Its dominance in the intertidal and shallow subtidal area of Suisun Bay is consistent with that opinion. Cluster 5 groups two stations (406 and 422), which have little in common with each other except for an abundance of *T. decipiens* but have less in common with other samples in the data set. They are distinguished from cluster 4, which is dominated by *T. decipiens,* because of high frequencies of a single species, rare or absent in other samples. *Cyclotella menegheniana* abounds at station 406 and *Diploneis decipiens* at station 422. Cluster 5 probably represents variation within the composite floral assemblage characterizing the deeper portions of Suisun Bay.

Stations in clusters 6a and 6b in San Pablo Bay show the highest number of species per sample (R, Table 1) in the data set reflecting the wide variety of species in the assemblages for those clusters. The dominant species are *Paralia sulcata* and *Thalassiosira decipiens,* and the ratio of these species distinguishes those two clusters. Stations in cluster 6b show high ratios of *Paralia sulcata* to *Thalassiosira decipiens,* and stations in cluster 6a exhibit lower ratios of *P. sulcata* (PS) to *T. decipiens* (TD). The PS/TD ratio decreases away from the margins, towards the channels, and upstream. This trend continues into Suisun Bay, where *P. sulcata* is almost nonexistent, and into San Francisco Bay, where *T. decipiens* is exceedingly rare. That distributional

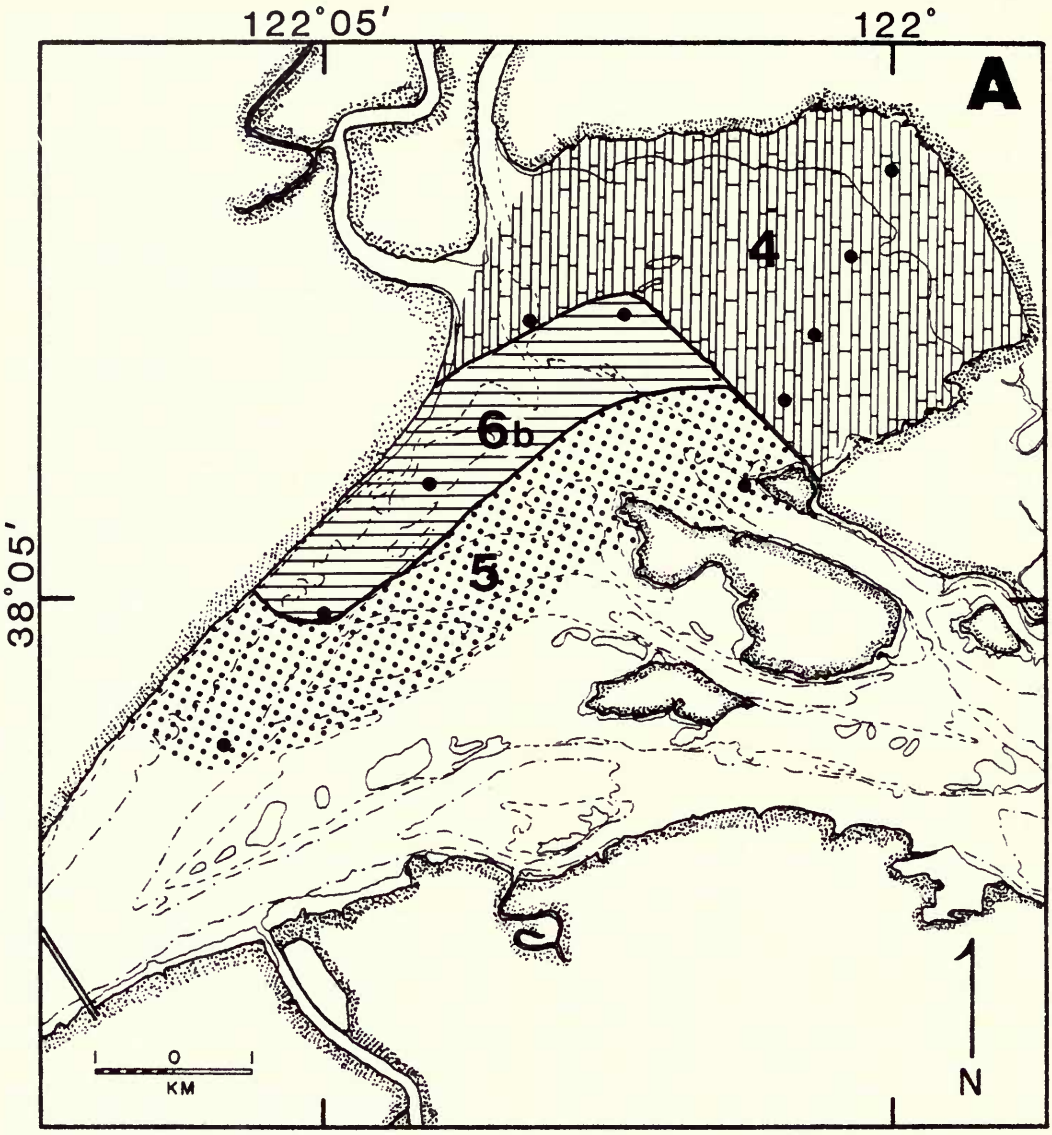


FIGURE 9. Distribution of Q-mode clusters in Suisun Bay.

pattern and the distinction between clusters 6a and 6b is also reflected in analysis of principal component scores (Fig. 16) as discussed below. The PS/TD ratio apparently varies directly with increasing salinity, and may serve as a salinity index in ancient nearshore deposits.

Principal Components

R-mode principal components analysis of the species frequency data extracted five components that account for 91.5% of the variance in the data. I examined those five components further because their interpretation corresponds well with the results of the Q-mode cluster analysis. However, no particularly large difference in eigenvalues between components 5 and 6 especially delimits the first five components. Components 6–32 account for the remaining 8.5% of the variance, and components 33–49 have near zero eigenvalues. Figure 15 shows the loadings for the first 5 principal components for 14 se-

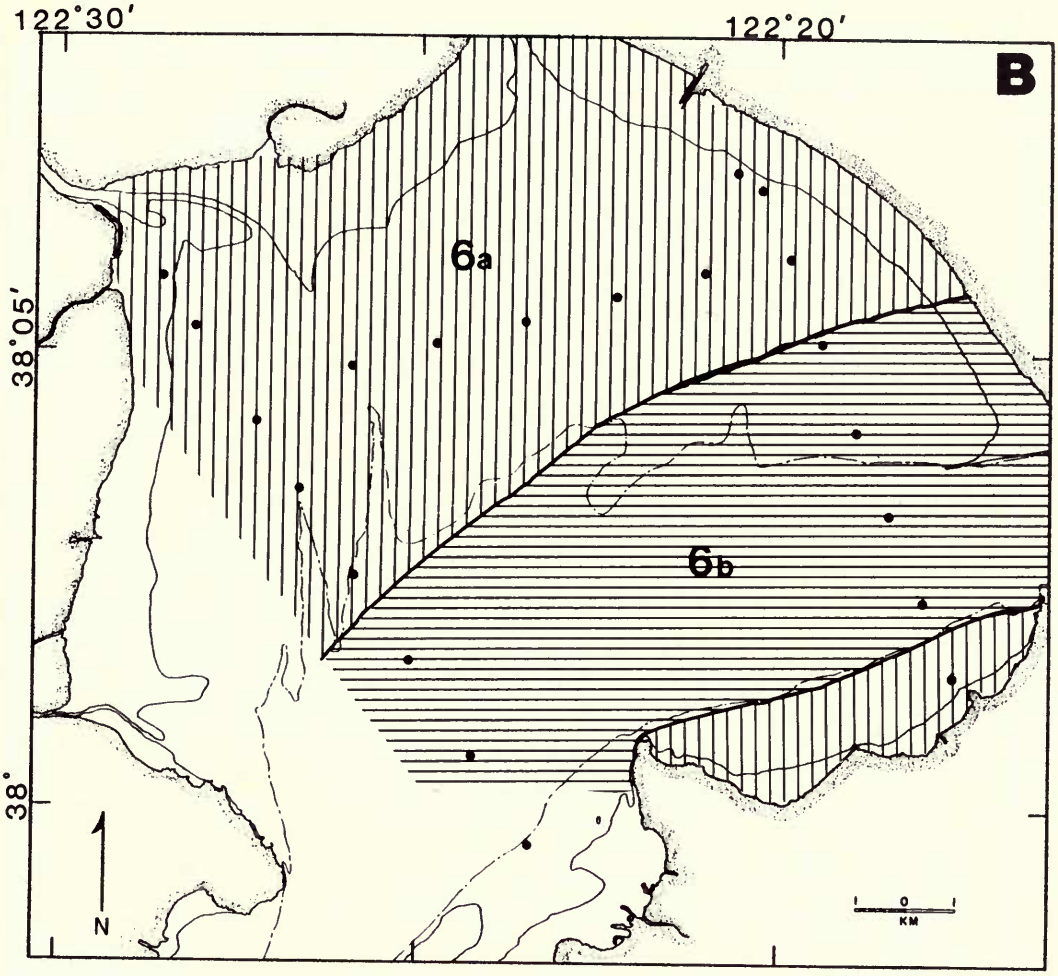


FIGURE 10. Distribution of Q-mode clusters in San Pablo Bay.

lected taxa. Figure 16 shows principal component (PC) scores for each station plotted for PC1 versus PC2 and PC4 versus PC5. Each station is coded according to the Q-mode cluster in which it belongs. Plots over other combinations of principal components show similar patterns, in particular with respect to the relationship between Q-mode clusters and principal components.

Principal component 1 accounts for 61.7% of the variance, and is characterized by *Thalassiosira decipiens* and *Fragilaria construens* (Fig. 15). Stations in clusters 4 and 6b show positive scores for PC1 (Fig. 16). PC1 represents a low-salinity component as evidenced by high scores for stations in Suisun Bay (Fig. 16). This component shows positive scores for stations in the main channel and deeper parts of San Pablo Bay; these scores probably result from intrusion of low-salinity water into San Pablo Bay through the main channel and the concomitant downstream transport of *T. decipiens*. A comparison of diatom frequency (abundance) suggests that this component characterizes areas of high diatom productivity (see Table 1).

PC2 explains 17.2% of the variance and has positive loadings for *Paralia sulcata, Ditylum brightwellii, Actinoptychus senarius,* and *Cyclotella striata/stylorum* (Fig. 15). This component has high positive scores for stations in the central part of southern San Francisco Bay (cluster 2, Fig. 16). This is a high salinity, deeper water component characterized by brackish-water and neritic marine, planktonic species.

PC3 explains 5.6% of the variance and is char-

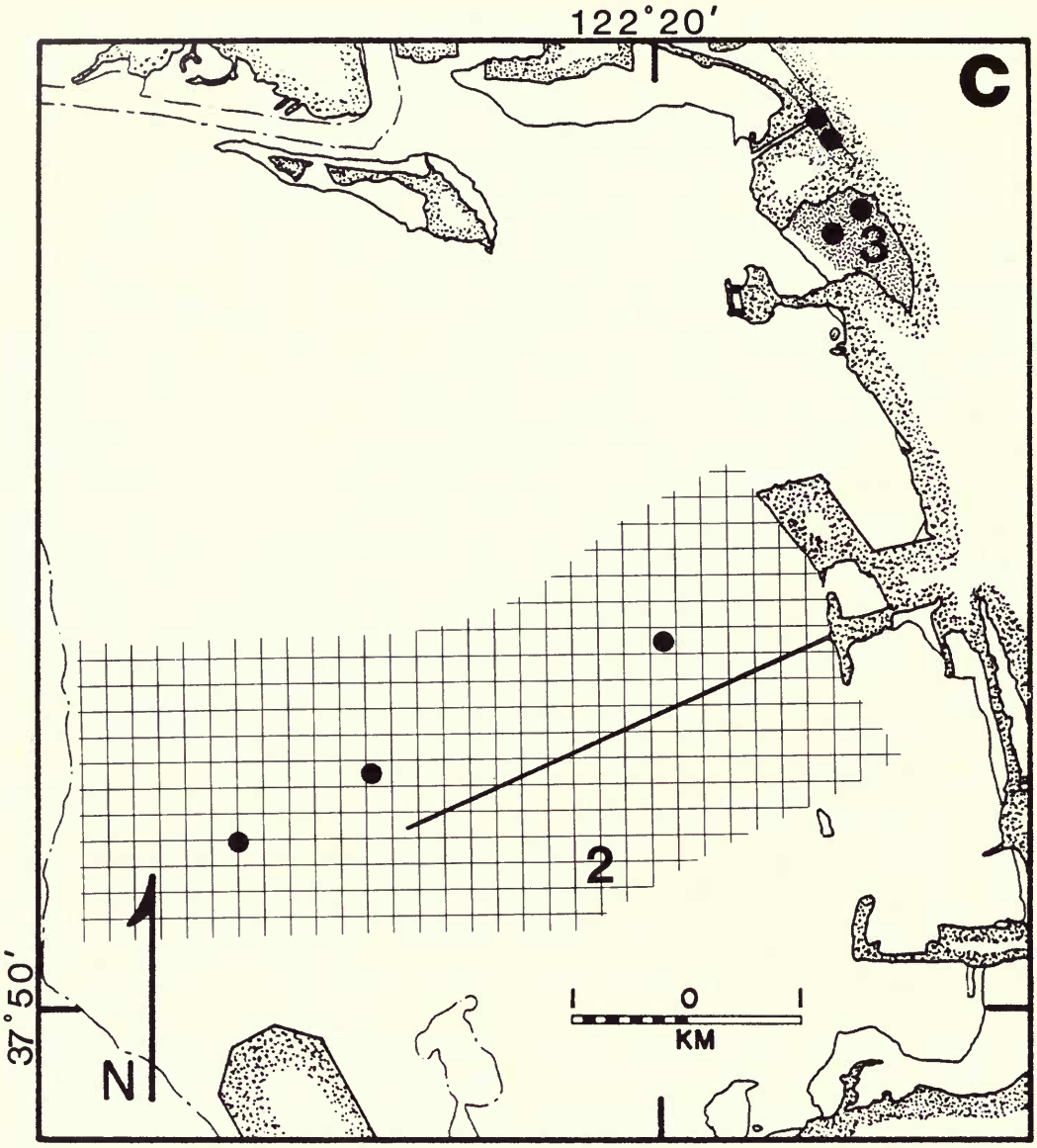


FIGURE 11. Distribution of Q-mode clusters in northern San Francisco Bay and Albany mud flats.

acterized by *Gyrosigma fasciola, Navicula tripunctata,* and *Nitzschia acuminata* (Fig. 15). Those marine-to-brackish-water epipelagic species define an intertidal to shallow subtidal, mud-flat component. Stations in cluster 1 in the shallow and marginal area of southern San Francisco Bay have high scores for this component. That pattern is very similar to the distribution of positive scores for PC4 (Fig. 16). PC4, characterized by *Nitzschia acuminata, N. pusilla, Bacillaria paxillifer,* and several other species (Fig. 15), accounts for 3.9% of the variance. These are marine-to-brackish-water epipelagic species typical of intertidal to subtidal mud flats in many coastal areas (Round 1971). PC4 is similar to PC3 in that they both represent intertidal to shallow subtidal, benthic components, and both show high scores for stations in southern San Francisco Bay (cluster 1, Fig. 16). However, PC4 shows higher scores for stations north of the San Mateo

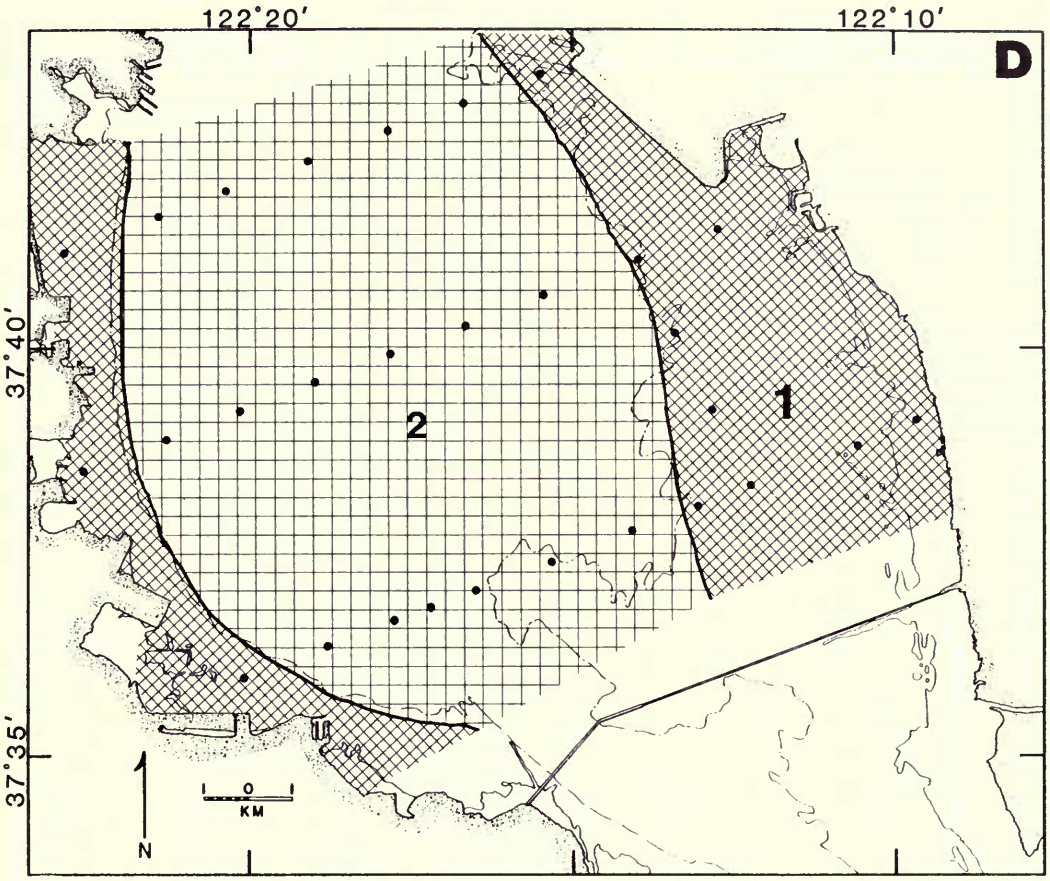


FIGURE 12. Distribution of Q-mode clusters in southern San Francisco Bay, north of Dumbarton Bridge.

Bridge, whereas PC3 prevails at stations in the areas south of the Dumbarton Bridge, reflecting the subtle differences in floral assemblages north and south of Dumbarton Bridge (Fig. 1, 14).

PC5 accounts for 3.1% of the variance and includes *Nitzschia sigmaformis,* and *Achnanthes haukiana* (Fig. 15). These are brackish-water-to-fresh-water benthic species. *Achnanthes haukiana* is very common and widespread in fresh to slightly brackish water (Patrick and Reimer 1966). *Nitzschia sigmaformis* has previously only been reported by Hustedt (1955) in mud samples from coastal areas of North Carolina. This component shows high scores for samples in cluster 3 (Fig. 16) which includes the Albany mud-flat and salt-marsh samples. This rather protected area in the intertidal zone is cut by several small fresh-water streams, which accounts for the low-salinity character. PC5 represents a low-salinity, high-intertidal-to-supratidal component. This component also appears to characterize areas of high diatom productivity based on comparisons of diatom frequency (Table 1).

DISCUSSION

A comparison of studies of diatoms in surface sediments from coastal areas in Oregon, the German Wadden Sea, Louisianna, South Africa, North Carolina, Sweden, and West Africa shows a range of 112 to 390 species (Hustedt 1955; Hendey 1958; Miller 1964; Giffen 1971, 1973, 1975; Amspoker and McIntire 1978; Colijn and Nienhuis 1978; Cook and Whipple 1982). The wide disparity in these figures reflects to a large degree, the range of habitats sampled in each study. Nevertheless, they provide estimated minimum and maximum values for numbers of species in coastal and estuarine sediments. The number of species (232) reported from surface

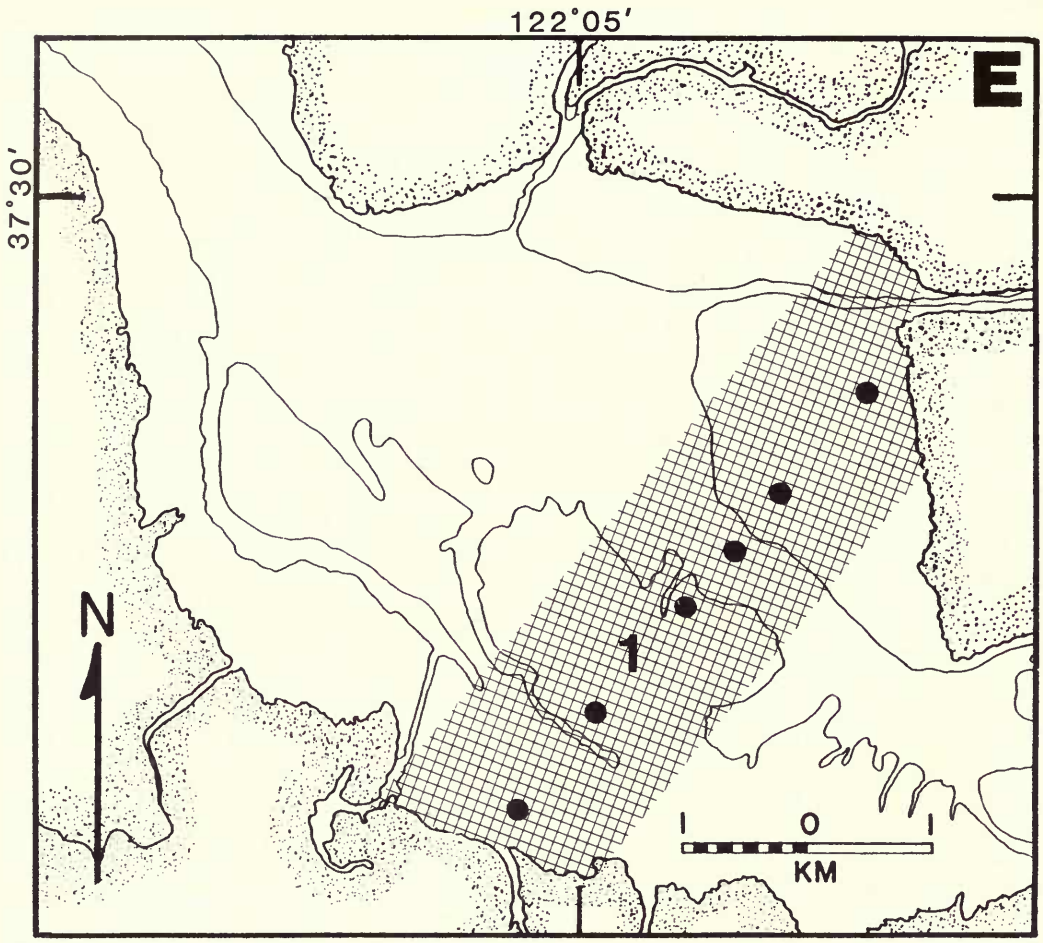


FIGURE 13. Distribution of Q-mode clusters in southern San Francisco Bay, south of Dumbarton Bridge.

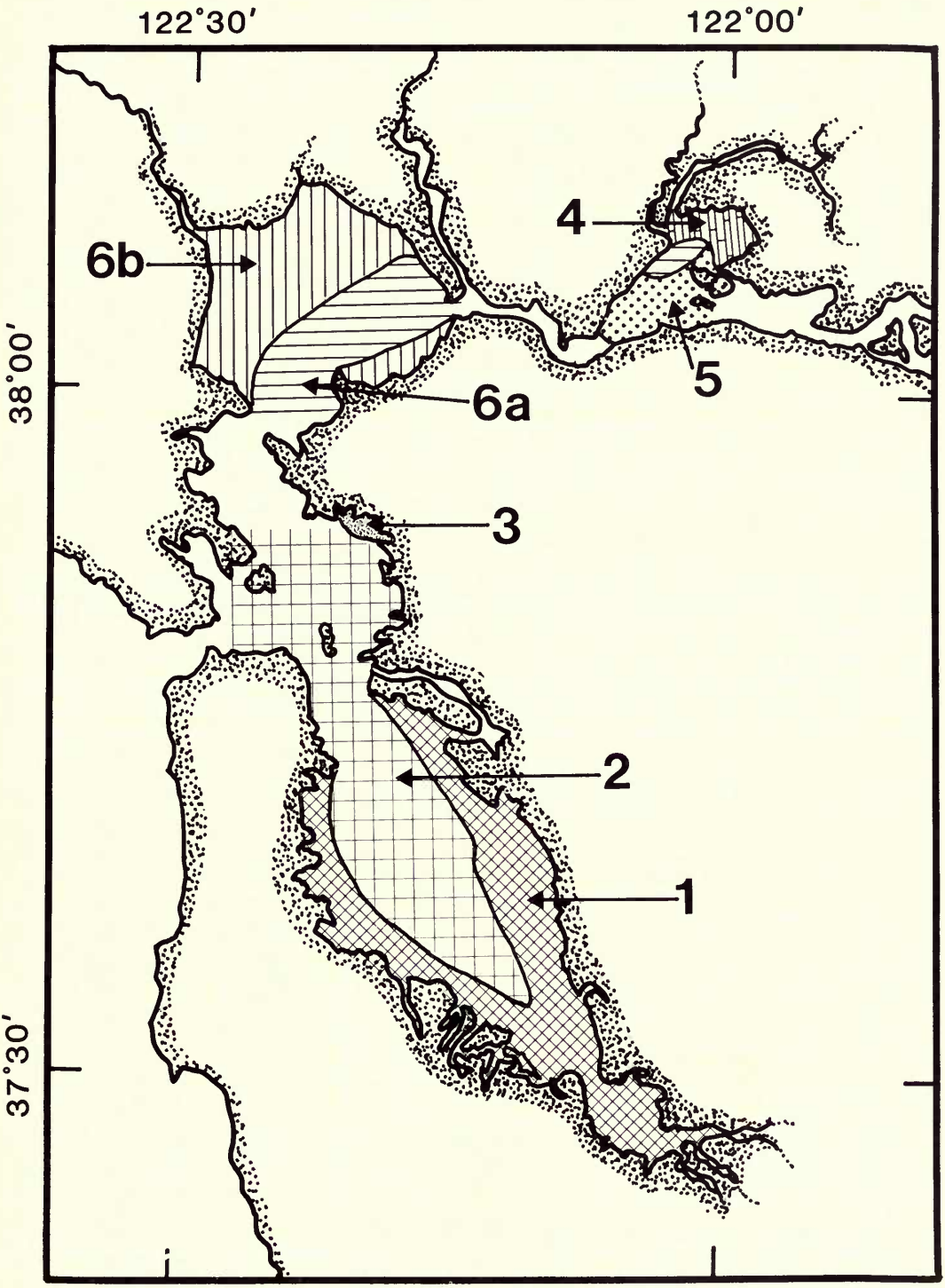
sediments in San Francisco Bay falls within that range and seems reasonable.

Significant patterns of diatom abundance and distribution in sediments of San Francisco Bay estuary include the following: (1) Highest diatom abundance is found in shallow subtidal to intertidal areas, especially in Suisun Bay and northern San Francisco Bay (Albany mud flats). (2) Areas of high species diversity (richness) in San Pablo Bay and southern San Francisco Bay do not correspond to areas of high abundance. (3) The distribution of species assemblages as determined by Q-mode cluster and R-mode principal components analysis follows gradients of salinity and depth. (4) Based on sediment analysis, the dominant (most abundant) species in the estuary are benthic or meroplanktonic and include *Thalassiosira decipiens, Paralia sulcata, Nitzschia acuminata, Melosira moniliformis,* and *Achnanthes haukiana.* (5) These results are consistent with distributional patterns of benthic microalgal biomass measured as chlorophyll-a and phaeophytin.

The distribution of diatoms along gradients of salinity and depth has been documented by numerous workers (e.g., Castenholz 1963, 1964, 1967; Round 1971; Amspoker and McIntire 1978; Colijn and Nienhuis 1978; McIntire 1978;

→

FIGURE 14. Distribution of Q-mode clusters throughout the San Francisco Bay Estuary system. Dominant or characteristic taxa are as follows: Cluster 1—*Nitzschia acuminata, Nitzschia pusilla;* Cluster 2—*Paralia sulcata, Ditylum brightwellii;* Cluster



3—*Nitzschia sigmaformis, Achnanthes haukiana;* Cluster 4—*Thalassiosira decipiens;* Cluster 5—*Thalassiosira decipiens, Cyclotella menegheniana;* Cluster 6a—*Thalassiosira decipiens, Paralia sulcata* (1:1); Cluster 6b—*Thalassiosira decipiens, Paralia sulcata* (6:1).

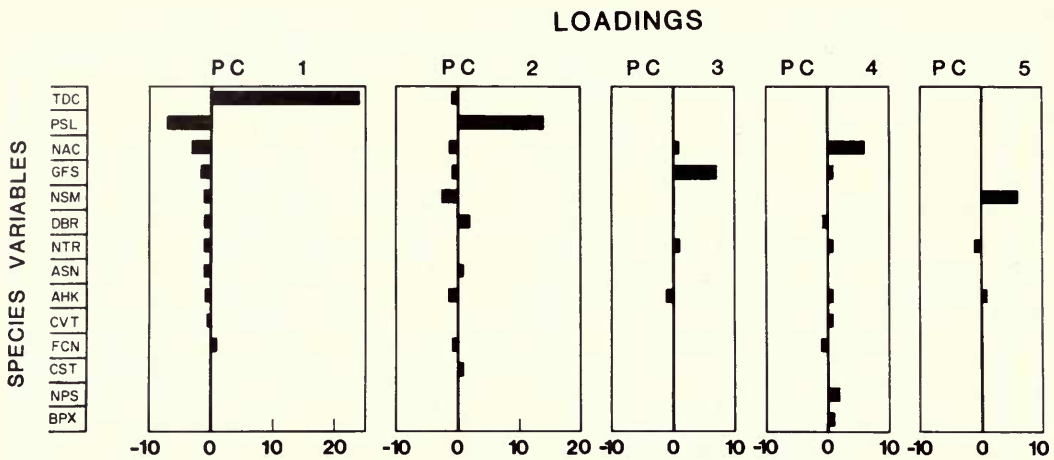


FIGURE 15. Principal component loadings for 14 selected species of the first five principal components. TDC = *Thalassiosira decipiens*, PSL = *Paralia sulcata*, NAC = *Nitzschia acuminata*, GFS = *Gyrosigma fasciola*, NSM = *Nitzschia sigmaformis*, DBR = *Ditylum brightwellii*, NTR = *Navicula tripunctata*, ASN = *Actinoptychus senarius*, AHK = *Achnanthes haukiana*, CVT = *Cocconeis vitrea*, FCN = *Fragilaria construens*, CST = *Cyclotella striata* ≠ *stylorum*, NPS = *Navicula pseudolanceolata*, BPX = *Bacillaria paxillifer*.

Colijn and Dijkema 1981). While salinity is probably the overriding control, the full significance of depth is rarely appreciated. Depth directly or indirectly controls parameters such as tidal exposure and immersion time, bottom sediment type, turbidity and resuspension, amount and wavelength of light penetration, and photoperiod. These parameters may also significantly affect the distribution and timing of the spring bloom in the San Francisco Bay estuary.

Amspoker and McIntire (1978) and Colijn and Dijkema (1981) attributed distributional patterns of diatom species to sediment type, reporting higher abundance with increasing silt and

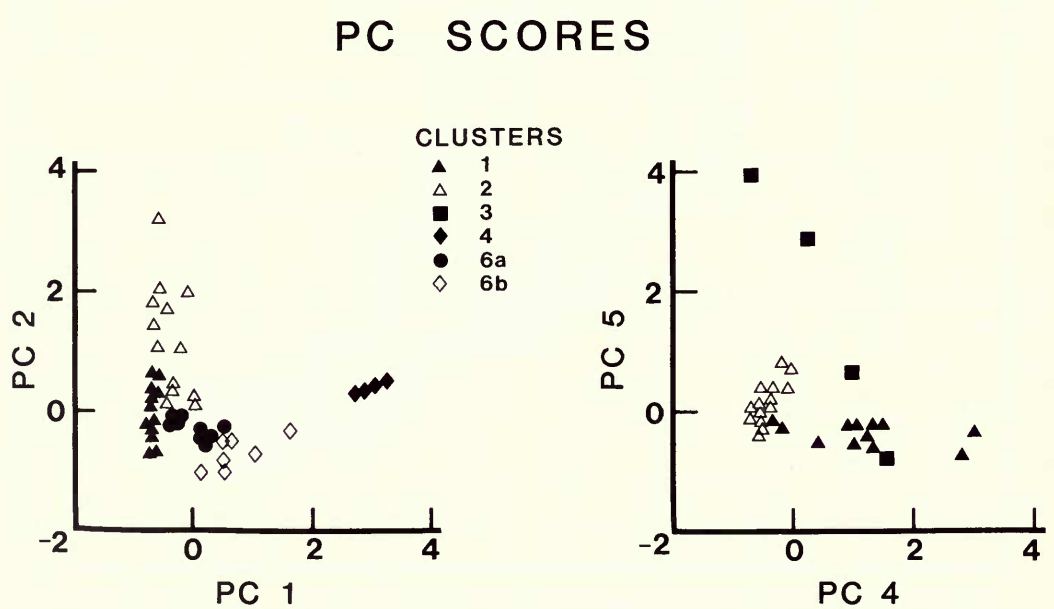


FIGURE 16. Principal component score scatter diagrams for components 1 versus 2 and components 4 versus 5. Each point represents a sampling station and is coded according to the Q-mode cluster with which it belongs.

clay. This pattern also appears in the San Francisco Bay estuary. However, this may reflect the predominance of fine-grained sediment in the easily accessible, marginal areas of the limited number of estuaries thus far sampled or the high organic content of these fine-grained sediments. Fine-grained sediment also indicates less-turbulent current regimes and therefore lower turbidity and higher light penetration. Castenholz (1963), McIntire and Overton (1971), and Main and McIntire (1974) demonstrated that length of exposure or immersion time is a fundamental control on the distribution of diatom assemblages. These studies employed natural or artificial substrates oriented perpendicular to sea level. The same effect is produced by tides along the bottom (a horizontal substrate) depending on location with respect to the bathymetric profile (depth).

Thompson and Laws (1982) attributed the distribution of benthic algal biomass and species composition to changes in light availability and resuspension. Peak biomass and diatom abundance, as represented by the samples described above, corresponds with minimal wind and tidal current velocities, hence low turbidity and high light penetration. During this period of high productivity in the shoals of the estuary, benthic taxa predominate. In contrast, biomass is low and meroplanktonic and planktonic species predominate during periods of high winds and tidal currents in winter and summer.

The spring bloom recorded in Suisun Bay has been attributed to the concentration of nutrients and particulate matter in the null zone (Arthur and Ball 1979; Cloern 1979). However, high production in the shoals and subsequent resuspension and seeding of the null zone may be a significant process. Concentration of these resuspended, benthic diatoms by the estuarine circulation in the null zone is a natural consequence. This is also indicated by the dominance of *Thalassiosira decipiens* during the bloom in Suisun Bay. The abundance of benthic diatoms in other shallow areas of San Francisco Bay suggests that the microphytobenthos is a significant contributor to total productivity in the estuary (Thompson et al. 1981).

The apparent lack of a corresponding spring diatom bloom in San Pablo Bay is puzzling (Thompson and Laws 1982). The high diversity results from the mixture of fresh and brackish-water species in that area. Fine-grained, river-borne material which escapes the entrapment zone and material transported upstream by tidal currents mix and are deposited in the mud flats of San Pablo Bay (Krone 1979).

Floral List

I identified two hundred seventy-three taxa while examining samples from the Yerba Buena mud and Recent surface sediment in the San Francisco Bay estuary. Undoubtedly many small, delicate, and rare taxa are omitted from this list, but the taxa reported here probably represent those that occur in significant abundance in sediments of the bay system.

Increased use of the electron microscope in recent years has led to substantial changes in nomenclature since the classic works of Hustedt (1927–1966), Cleve-Euler (1951–1955), Hendey (1964), and Patrick and Reimer (1966, 1975). Every attempt was made to incorporate those changes into the taxonomy presented here. Simonsen (1979) summarized many of those changes, and I followed his classification. Other recent taxonomic revisions included in this list are those of Cox (1979), Lange-Bertalot (1977, 1980*a, b*), Lange-Bertalot and Simonsen (1978), and Schmid (1977).

Written descriptions for each taxon are not provided because in nearly every case they are currently available in the literature. The particular references used for each specific identification are given. However, those taxa treated under an open numerical system or as indeterminate include appropriate descriptive and comparative comments. Ecological parameters of each taxon, based largely on published data on salinity tolerance and life habits, are given when possible. Salinity tolerance is given according to the system of Simonsen (1962) (Fig. 17). Detailed data on abundance and distribution is provided in Laws (1983*b*).

All illustrations are valve views unless otherwise stated. Photographs were taken with an Olympus BH-2, PM-10AD photomicrography system using 50× and 100× oil-immersion lenses and Nomarski interference contrast. The following abbreviations appear in the plate descriptions: RV = raphe valve, PRV = pseudoraphe valve, L = length, D = diameter. Each figure number refers to a different specimen. Lowercase letters refer to different views (focal planes or magnifications) of the same specimen.

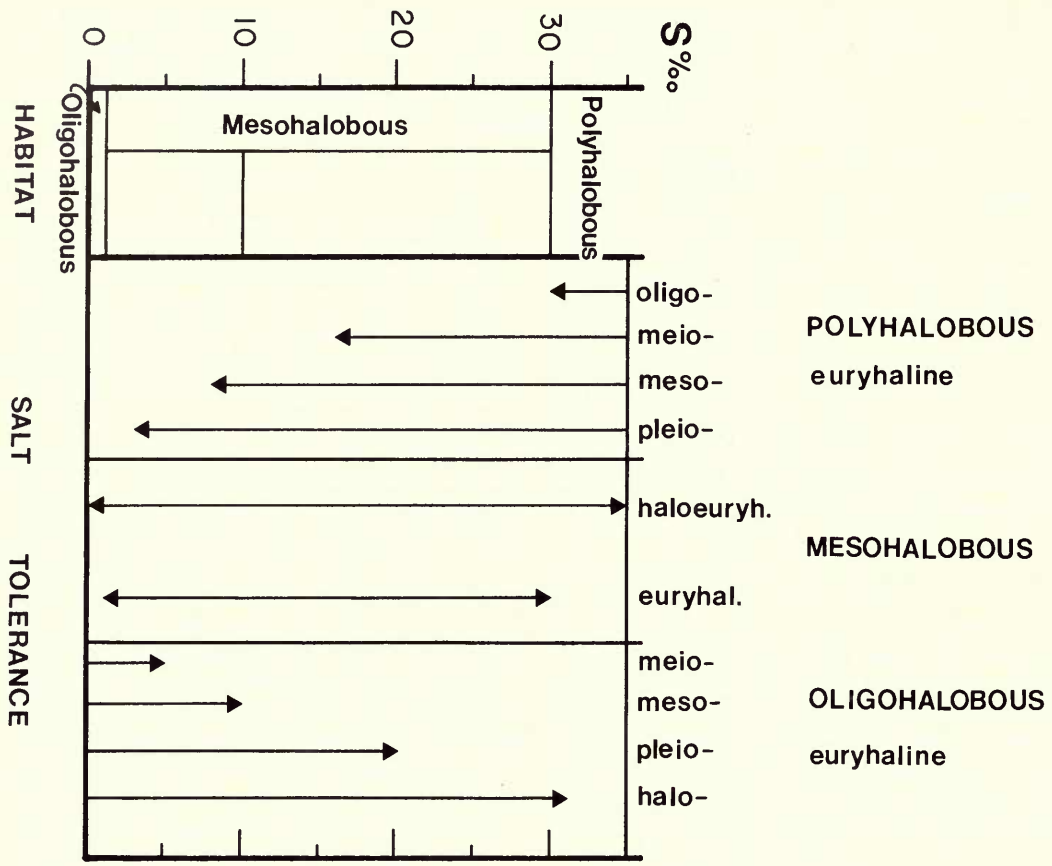


FIGURE 17. Salinity tolerance and habitat classification according to the "halobien" spectra of Simonsen (1962).

Bulk material and representative strewn mounts of each sample examined in this study are archived at the Museum of Paleontology, University of California, Berkeley.

Achnanthes Bory, 1822

Achnanthes brevipes Agardh, 1824

(Pl. 17, Fig. 22)

DESCRIPTION.—Hustedt 1933b:424–426, fig. 877.
ECOLOGY.—Mesohalobous, euryhaline (Pankow 1976; Schrader 1978); benthic.
DISTRIBUTION.—On intertidal mud flats and salt marsh of Central Bay, Sangamon, and Recent.

Achnanthes brevipes var. *intermedia* (Kutzing) Cleve, 1895

(Pl. 17, Fig. 17–19)

DESCRIPTION.—McIntire and Reimer 1974:171; pl. 2, fig. 8; pl. 3, fig. 2.
ECOLOGY.—Brackish water, benthic.
DISTRIBUTION.—Present in Sangamon and Recent sediments, not abundant.

Achnanthes conspicua var. *brevistriata* Hustedt, 1930*b*

(Pl. 17, Fig. 9)

DESCRIPTION.—Hustedt 1933:387, fig. 833e–f.
ECOLOGY.—A freshwater species (Hustedt 1933).
DISTRIBUTION.—Rare in San Pablo Bay; Recent.

REMARKS.—The specimens from San Francisco Bay have somewhat coarser striae (8 in 10 μm) than described by Hustedt for *A. conspicua* (13–14 in 10 μm).

Achnanthes groenlandica var. *phinneyi* McIntire and Reimer, 1974

(Pl. 17, Fig. 16)

DESCRIPTION.—McIntire and Reimer 1974:172, pl. 2, fig. 3a–c; pl. 3, fig. 3a, b.
ECOLOGY.—Brackish water, benthic.
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Achnanthes haukiana Grunow, 1880

(Pl. 17, Fig. 14)

DESCRIPTION.—Patrick and Reimer 1966:267–269, pl. 17, fig. 25–32.

ECOLOGY.—Mesohalobous, euryhaline (Pankow 1976); fresh to moderately brackish water (Patrick and Reimer 1966).

DISTRIBUTION.—Intertidal mud flats near areas where creeks enter the Bay. Recent.

Achnanthes haukiana var. *rostrata* Schulz, 1926

(Pl. 17, Fig. 11–13, 15)

DESCRIPTION.—Patrick and Reimer 1966:269, pl. 17, fig. 33, 34.

ECOLOGY.—Same as species.

DISTRIBUTION.—Same as species.

Achnanthes lanceolata Brébisson *in* Kutzing, 1846

(Pl. 17, Fig. 20, 21; Pl. 25, Fig. 8, 9)

DESCRIPTION.—Patrick and Reimer 1966:269–270, pl. 18, fig. 1–10.

ECOLOGY.—Widespread in fresh and brackish water. Fresh water (Hustedt 1933), brackish water (Hendey 1964).

DISTRIBUTION.—On intertidal mud flats throughout the Bay; Sangamon and Recent.

Achnanthes longipes Agardh, 1824

(Pl. 17, Fig. 23a, b)

DESCRIPTION.—Hendey 1964:174, pl. 28, fig. 1–6; pl. 42, fig. 2.

ECOLOGY.—Benthic, littoral marine, prefers salinities of 32–34‰ (Hendey 1964).

DISTRIBUTION.—Rare in Recent sediments.

Achnanthes parvula Kutzing, 1844

(Pl. 18, Fig. 2)

DESCRIPTION.—McIntire and Reimer 1974:174, pl. 2, fig. 4a, b; pl. 4, fig. 3a–d.

ECOLOGY.—Brackish water, neritic, benthic.

DISTRIBUTION.—Intertidal mud flat, Central Bay; Recent sediments.

Achnanthes wellsiae Reimer *in* Patrick and Reimer, 1966

(Pl. 17, Fig. 10; Pl. 18, Fig. 3)

DESCRIPTION.—Patrick and Reimer (1966):255, pl. 16, fig. 14–17.

ECOLOGY.—Poorly known, only reported from brackish water.

DISTRIBUTION.—In one intertidal salt-marsh sample. Recent sediments.

Achnanthes yaquinensis McIntire and Reimer, 1974

(Pl. 18, Fig. 1)

DESCRIPTION.—McIntire and Reimer 1974:174; pl. 2, fig. 1a, b; pl. 3, fig. 1a, b.

ECOLOGY.—Brackish water, benthic.

DISTRIBUTION.—Intertidal mud flat, Recent sediments.

Actinocyclus Ehrenberg, 1837

Actinocyclus normanii (Gregory) Hustedt, 1957

(Pl. 8, Fig. 1–3, 7, 9, 11, 12)

DESCRIPTION.—Hustedt 1957:218, fig. 5, 6.

ECOLOGY.—Planktonic, mesohalobous (Schrader 1978); polyhalobous, mesoeuryhaline (Pankow 1976); marine to brackish (Hasle 1977).

DISTRIBUTION.—Abundant in Yerba Buena mud; present but rare in Recent sediments.

Actinocyclus normanii f. *subsalsa* (Juhlin.-Dannt.) Hustedt, 1957

(Pl. 8, Fig. 4–6, 8, 10)

DESCRIPTION.—Hasle 1977:321–328, fig. 1, 3–10, 18, 19, 22, 23.

ECOLOGY.—Fresh to moderately brackish water, indicative of high eutrophication and pollution (Hasle 1977; Stoermer and Yang 1969).

DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Actinocyclus octanarius Ehrenberg, 1838

(Pl. 9, Fig. 1, 5)

DESCRIPTION.—Hendey 1964:83, pl. 24, fig. 3.

ECOLOGY.—Planktonic, polyhalobous (meso- to meioeuryhaline (Pankow 1976).

DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Actinocyclus? sp. 1

(Pl. 9, Fig. 2)

DESCRIPTION.—Valve circular, strongly convex, central area large, about ½ the diameter with irregularly scattered punctae; remaining portion of valve covered with widely spaced, coarsely punctate striae, 6 in 10 μm, diameter is 31 μm.

DISTRIBUTION.—A single specimen from the Yerba Buena mud.

Actinoptychus Ehrenberg, 1841

Actinoptychus senarius Ehrenberg, 1838

(Pl. 13, Fig. 1–4, 7)

DESCRIPTION.—Hendey 1964:95, pl. 23, fig. 1, 2.

ECOLOGY.—Planktonic, polyhalobous, meioeuryhaline (Pankow 1976); cosmopolitan in neritic plankton (Hendey 1964); meroplanktonic (Schuette and Schrader 1979).

DISTRIBUTION.—Common in Sangamon sediment and present in Recent sediment.

REMARKS.—This species is abundant in samples from the upper part of the Yerba Buena muds and commonly occurs with *Thalassionema nitzschioides* in the Yerba Buena muds. Hendey (1964) states that *A. senarius* is always present, but never abundant, in neritic plankton

samples worldwide. It is curious, therefore, to find it as the dominant species in some samples.

Actinoptychus splendens (Shadbolt) Ralfs *in* Pritchard, 1861
(Pl. 13, Fig. 5, 6)

DESCRIPTION.—Hendey 1964:95, pl. 22, fig. 1.
ECOLOGY.—Same as *A. senarius*.
DISTRIBUTION.—Rare in Sangamon and Recent sediment.

Amphipleura Kutzing, 1844

Amphipleura rutilans (Trent.) Cleve, 1894
(Pl. 19, Fig. 4, 7)

DESCRIPTION.—Patrick and Reimer 1966:304, pl. 21, fig. 3.
ECOLOGY.—Lives in gelatinous tubes attached to bottom.
DISTRIBUTION.—Intertidal mud flats and salt-marsh sediments of Recent bay.

Amphora (Ehrenberg) Kutzing, 1844

Amphora ovalis (Kutzing) Kutzing, 1844
(Pl. 27, Fig. 4)

DESCRIPTION.—Patrick and Reimer 1966, pl. 13, fig. 1, 2.
ECOLOGY.—Benthic, oligohalobous mesoeuryhaline (Pankow 1976); alkaliphilous (Patrick and Reimer 1966).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Amphora granulata Gregory, 1857
(Pl. 27, Fig. 5, 7, 8)

DESCRIPTION.—Cleve-Euler 1953:100. Hustedt 1955:40, pl. 14, fig. 8–10, 26, 27.
ECOLOGY.—Benthic, marine (Hendey 1964).
DISTRIBUTION.—Recent sediment, rare.

Amphora sublaevis Hustedt, 1955
(Pl. 27, Fig. 10)

DESCRIPTION.—Hustedt 1955:41, pl. 13, fig. 3, 12–15.
DISTRIBUTION.—Intertidal mud flats and salt marsh, epiphytic; from Recent sediment, abundant in some samples.

Amphora ventricosa (Gregory) Hendey, 1951
(Pl. 27, Fig. 9)

DESCRIPTION.—Hendey 1951:70, pl. 9, fig. 6. Hendey 1964: 269, pl. 38, fig. 12.
ECOLOGY.—Marine to brackish water, littoral, benthic (Hendey 1964).
DISTRIBUTION.—Frequent and widespread in Recent sediments, especially from intertidal mud flats and salt marshes in central and southern San Francisco Bay.

Amphora sp. 1
(Pl. 27, Fig. 6)

DESCRIPTION.—Valves semi-lanceolate, ends rounded and directed slightly ventrally, ventral margin straight, slightly inflated in the middle of the valve, dorsal margin convex, raphe arcuate, central area very narrow, central nodule small, valve striate, striae parallel becoming slightly convergent near the end, very fine 25–30 in 10 μm, length is 30–45 μm, breadth is 5–8 μm.
DISTRIBUTION.—Intertidal mud flats, Recent sediment.

Anomoeoneis Pfitzer, 1871

Anomoeoneis sphaerophora f. *costata* (Kutzing) Schmid, 1977
(Pl. 22, Fig. 3)

DESCRIPTION.—Patrick and Reimer 1966:376, pl. 32, fig. 3. Schmid 1977:320, pl. 3, fig. 13–20.
ECOLOGY.—Benthic, mesohalobous (Pankow 1976); in waters of moderate to high salt concentration (Patrick and Reimer 1966).
DISTRIBUTION.—Rare, Sangamon sediment.

Arachnoidiscus Bailey, 1849

Arachnoidiscus ehrenbergi Bailey, 1849
(Pl. 14, Fig. 5)

DESCRIPTION.—Hustedt 1929:471, fig. 262.
ECOLOGY.—A coastal marine species, commonly found in association with *Isthmia* spp. (Hustedt 1929). Epiphytic, rarely found in plankton (Gran and Angst 1931).
DISTRIBUTION.—Present in Sangamon and Recent sediment, commonly associated with *Isthmia nervosa*.

Asteromphalus Ehrenberg, 1844

Only one poorly preserved specimen was recorded from Recent and Sangamon sediments and was not treated taxonomically.

Aulacosira Thwaites, 1848

Aulacosira ambigua (Grunow) Simonsen, 1979
(Pl. 1, Fig. 8)

DESCRIPTION.—Hustedt 1927:256, fig. 108.
ECOLOGY.—Oligohalobous, meioeuryhaline (Pankow 1976).
DISTRIBUTION.—Rare in Sangamon sediment.

Aulacosira granulata (Ehr.) Simonsen, 1979
(Pl. 1, Fig. 11–15)

DESCRIPTION.—Hustedt 1927:248, fig. 104.
ECOLOGY.—Oligohalobous, meioeuryhaline (Pankow 1976); plankton in eutrophic fresh water (Hustedt 1927).
DISTRIBUTION.—Recent and Sangamon sediment, rare.

Aulacosira islandica (O. Muller) Simonsen, 1979
(Pl. 2, Fig. 2–4)

DESCRIPTION.—Hustedt 1927:252, fig. 106, 107.
ECOLOGY.—Oligohalobous, meioeuryhaline (Pankow 1976), "very abundant and widespread in eutrophic fresh water. . . . " (Hustedt 1927).
DISTRIBUTION.—Recent and Sangamon sediments.

Aulacosira italica (Ehrenberg) Simonsen, 1979
(Pl. 1, Fig. 9, 10)

DESCRIPTION.—Hustedt 1927:257, fig. 109.
ECOLOGY.—Littoral of freshwater streams and lakes (Hustedt 1927).
DISTRIBUTION.—Rare in Recent and Sangamon sediments.

Auricula Castracane, 1875

Auricula complexa Gregory, 1857
(Pl. 29, Fig. 14)

DESCRIPTION.—Pankow 1976:145, fig. 295.
ECOLOGY.—Polyhalobous, meioeuryhaline, subtropical, benthic (Pankow 1976).
DISTRIBUTION.—A single specimen in Recent sediments from Albany mud flats.

Bacillaria Gmelin, 1788

Bacillaria paxillifer (O. F. Müller) Hendey, 1951
(Pl. 31, Fig. 2)

DESCRIPTION.—Hendey 1951:74. Hustedt 1930*b*:396, fig. 755.
ECOLOGY.—Mesohalobous, holoeuryhaline (Pankow 1976).
DISTRIBUTION.—Present in Sangamon and Recent sediments.

Biddulphia Gray, 1821

Biddulphia alterans (Bailey) Van Heurck, 1880–1885
(Pl. 14, Fig. 2)

DESCRIPTION.—Hendey 1964:102, pl. 25, fig. 5.
ECOLOGY.—Neritic marine, benthic.
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Biddulphia aurita (Lyngbye) Brébisson, 1838
(Pl. 13, Fig. 8–10)

DESCRIPTION.—Hustedt 1930*a*:846, fig. 501, 502. Schmidt 1874, pl. 120, fig. 7–10; pl. 122, fig. 1–9.
ECOLOGY.—Polyhalobous, meioeuryhaline (Pankow 1976); neritic plankton (Hendey 1951).
DISTRIBUTION.—Frequent in Sangamon and Recent sediment.

Biddulphia laevis Ehrenberg, 1843
(Pl. 14, Fig. 1)

DESCRIPTION.—Hustedt 1930*a*:852, fig. 506, 507.
ECOLOGY.—Poorly known, mesohalobous(?) (Pankow 1976). It appears to be a coastal species that prefers moderately high salt concentrations.
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Caloneis Cleve, 1894

Caloneis alpestris (Grunow) Cleve, 1894
(Pl. 22, Fig. 8)

DESCRIPTION.—Patrick and Reimer 1966:587, pl. 54, fig. 9.
ECOLOGY.—Prefers cool, fresh, mesotrophic waters (Patrick and Reimer 1966), oligohalobous.
DISTRIBUTION.—Rare in Recent sediments.

Caloneis amphisbaena (Bory) Cleve, 1894
(Pl. 22, Fig. 10)

DESCRIPTION.—Patrick and Reimer 1966:579, pl. 53, fig. 2.
ECOLOGY.—Oligohalobous (indifferent), meioeuryhaline, in brackish and fresh water, benthic (Pankow 1976); fresh to slightly brackish water (Patrick and Reimer 1966).
DISTRIBUTION.—Rare in Recent sediment.

Caloneis bacillum (Grunow) Cleve, 1894
(Pl. 22, Fig. 6, 11)

DESCRIPTION.—Patrick and Reimer 1966:586, pl. 54, fig. 8.
ECOLOGY.—Oligohalobous, mesoeuryhaline, benthic, widely distributed in fresh waters (Pankow 1976).
DISTRIBUTION.—Rare in Sangamon and Recent sediment.

Caloneis ventricosa (Ehrenberg) Meister, 1912
(Pl. 22, Fig. 14)

DESCRIPTION.—Patrick and Reimer 1966:583, pl. 54, fig. 3.
ECOLOGY.—Fresh water, benthic.
DISTRIBUTION.—A single specimen from Sangamon sediments.

Caloneis westii (Smith) Hendey, 1964
(Pl. 22, Fig. 4, 5, 9)

DESCRIPTION.—Hendey 1964:230, pl. 44, fig. 5–10; pl. 45, fig. 1–13.
ECOLOGY.—Mesohalobous, euryhaline (Pankow 1976); a brackish-water species, common in the littoral zone (Hendey 1964); benthic.
DISTRIBUTION.—Common in Sangamon sediments and intertidal mud flats and salt marshes of present bay.

REMARKS.—This species is frequent in many Sangamon sediment samples. It is commonly found in association with *Nitzschia granulata* in Recent and Sangamon sediments.

Campylodiscus Ehrenberg, 1840

Campylodiscus clypeus Ehrenberg, 1840
(Pl. 35, Fig. 2)

DESCRIPTION.—Pankow 1976:319. Cleve-Euler 1952:128, fig. 1579.
ECOLOGY.—Mesohalobous (Pankow 1976), benthic.
DISTRIBUTION.—Rare in Recent sediments.

Campylodiscus echeneis Ehrenberg, 1840
(Pl. 35, Fig. 1, 3)

DESCRIPTION.—Hendey 1964:291, pl. 40, fig. 14.
ECOLOGY.—Mesohalobous (Pankow 1976); a common marine and brackish water species (Hendey 1964); a coastal marine species sometimes found in inland salt waters (Cholnoky 1968), benthic.

DISTRIBUTION.—Present in Sangamon and Recent sediment, not abundant.

REMARKS.—Sloan (1981) reports abundant *C. echeneis* in some Sangamon sediments from San Francisco Bay. The high density of *C. echeneis* observed by Sloan (1981) may be an artifact of sieving and sample concentration.

Campylodiscus incertus Schmidt, 1874
(Pl. 33, Fig. 19)

DESCRIPTION.—Schmidt 1874, Pl. 15, fig. 13–15, 19, 20; pl. 207, fig. 14. Giffen 1971:4, fig. 60.
DISTRIBUTION.—Rare in Recent sediments from intertidal mud flats and salt marshes, Albany mud flats.

Campylodiscus ralfsii Smith, 1853
(Pl. 33, Fig. 12)

DESCRIPTION.—Hendey 1964:291. Cleve-Euler 1952:127, fig. 1576.
ECOLOGY.—Mesohalobous, benthic.
DISTRIBUTION.—Rare in intertidal salt-marsh and mud flat sediments, Recent.

Cerataulus Ehr. 1843

Cerataulus turgidus (Ehrenberg) Ehrenberg, 1843
(Pl. 14, Fig. 10)

DESCRIPTION.—Hendey 1964:106, pl. 20, fig. 4.
ECOLOGY.—Polyhalobous, meioeuryhaline, planktonic and benthic (Pankow 1976).
DISTRIBUTION.—In Recent and Sangamon sediment, rare.

Chaetoceros Ehrenberg, 1844

Chaetoceros cinctus Gran, 1897
(Pl. 15, Fig. 1)

DESCRIPTION.—Cupp 1943:142, fig. 98.
ECOLOGY.—Polyhalobous, meioeuryhaline (Pankow 1976).
DISTRIBUTION.—Rare in Recent and Sangamon sediment.

REMARKS.—Hendey (1964) distinguishes this species from *C. radicans* by the lack of spines on the setae, whereas Cupp (1943) shows smooth setae in both species.

Chaetoceras mitra (Bailey) Cleve, 1896
(Pl. 15, Fig. 4)

DESCRIPTION.—Hendey 1964:124, pl. 16, fig. 2.
ECOLOGY.—Polyhalobous, meioeuryhaline.
DISTRIBUTION.—A single specimen from the Yerba Buena mud.

REMARKS.—Hendey (1964) distinguished resting spores of this species from the similar *C. lorenzianus* (Grunow) by its short conical protuberances. Hendey (1964:124, pl. 16, fig. 1) described *C. lorenzianus* as possessing elongate, curved protuberances on the resting spores. Gran and Angst (1931:471, fig. 53b, c) identified both forms as *C. lorenzianus*. Cupp (1943:118, fig. 71e, f) described *C. lorenzianus* resting spores with short protuberances. Evidently Gran and Angst (1931) and Cupp (1943) combined the two forms using the earlier epithet. Hendey (1964) recognized Cleve's (1896) distinction between *C. mitra* and *C. lorenzianus*.

Chaetoceros sp. 1
(Pl. 15, Fig. 2)

DESCRIPTION.—Resting spore, semispherical with numerous short spines scattered on convex surface. Diameter is 17 μm. This specimen is very similar to one illustrated by Schrader (1973, pl. 17, fig. 9–11).
DISTRIBUTION.—A single specimen in the Yerba Buena mud.

REMARKS.—No positive identification could be made from this specimen. Many species of *Chaetoceros* show similar resting spores.

Chaetoceros? sp. 2
(Pl. 15, Fig. 3)

DESCRIPTION.—Valve roughly semi-ovoid, somewhat expanded at the base; three large, hollow spines protrude from the rounded top; valve surface covered with longitudinal rows of coarse punctae; length is 17 μm; breadth is 15 μm.

REMARKS.—This specimen is questionably assigned to *Chaetoceros*. Valves of *Chaetoceros* only have two setae and the spines of resting spores are rarely as long as those of this specimen.

Cocconeis Ehrenberg, 1837

Cocconeis californica (Grunow) Cleve, 1895
(Pl. 18, Fig. 13, 14)

DESCRIPTION.—Hustedt 1933:343, fig. 796.
ECOLOGY.—Littoral, marine species, benthic (Hustedt 1933).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Cocconeis decipiens Cleve, 1873
(Pl. 18, Fig. 15)

DESCRIPTION.—Hustedt 1933:353, fig. 808.
ECOLOGY.—Coastal marine species, benthic (Hustedt 1933).
DISTRIBUTION.—A single specimen from the Yerba Buena mud.

Cocconeis diminuta Pantocsek, 1902
(Pl. 18, Fig. 10–12)

DESCRIPTION.—Hustedt 1933:346, fig. 800.
ECOLOGY.—Poorly known, probably fresh water, benthic.
DISTRIBUTION.—Rare in Recent and Sangamon sediments.

Cocconeis fasciolata Ehrenberg, 1844

(Pl. 19, Fig. 1, 2)

DESCRIPTION.—Brown 1920:232.
ECOLOGY.—Unknown.
DISTRIBUTION.—Rare but widely distributed in Sangamon and Recent sediments.

Cocconeis placentula Ehrenberg, 1838

(Pl. 18, Fig. 5, 6)

DESCRIPTION.—Patrick and Reimer 1966:240, pl. 15, fig. 7.
ECOLOGY.—Oligohalobous, holo- to pleioeuryhaline, a freshwater species (Pankow 1976); a widespread, epiphytic species, apparently salt indifferent (Patrick and Reimer 1966).
DISTRIBUTION.—Widespread but not abundant in Recent and Sangamon sediments.

Cocconeis scutellum Ehrenberg, 1837

(Pl. 18, Fig. 4; Pl. 19, Fig. 5)

DESCRIPTION.—Hustedt 1933:337, fig. 790.
ECOLOGY.—Polyhalobous, meio- to pleioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Present in Recent and Sangamon sediment, not abundant.

Cocconeis vitrea Brun, 1891

(Pl. 18, Fig. 7–9)

DESCRIPTION.—Brun 1891:19, pl. 18, fig. 2.
ECOLOGY.—Poorly known.
DISTRIBUTION.—Common in intertidal mud flats of present bay, rare in the Yerba Buena mud.

Cocconeis sp. 1

(Pl. 18, Fig. 16)

DESCRIPTION.—Pseudoraphe valve elliptical, saddle shaped. Axial area narrow and straight; valve surface striate, striae radial and moniliform; broadly spaced punctae form irregular longitudinal lines. Length is 19 μm; width is 16 μm; striae 16 in 10 μm.
DISTRIBUTION.—Rare in recent sediments from San Pablo Bay.

Cocconeis sp. 2

(Pl. 19, Fig. 3)

DESCRIPTION.—Pseudoraphe valve elliptical, flat. Axial area narrow, lanceolate. Valve surface striate, striae radial, punctate. Longitudinal line present parallel to the valve margin about ⅓ the width from the margin on each side of the valve. Length is 15 μm, width is 10 μm, striae 14 in 10 μm.
DISTRIBUTION.—A single specimen from Recent sediment of Albany mud flats.

Coscinodiscus Ehrenberg, 1838

Coscinodiscus curvatulus Grunow, 1878

(Pl. 9, Fig. 3, 4)

DESCRIPTION.—Hendey 1964:81. Hustedt 1928:406, fig. 214.
ECOLOGY.—Marine neritic, boreal, planktonic.
DISTRIBUTION.—Rare in Recent and Sangamon sediment.

Coscinodiscus decrescens Grunow *in* Schmidt, 1878

(Pl. 5, Fig. 3, 5)

DESCRIPTION.—Hustedt 1928:430, fig. 233.
ECOLOGY.—Coastal, marine plankton (Hustedt 1928).
DISTRIBUTION.—Rare in Yerba Buena mud.

Coscinodiscus jonesianus (Greville) Ostenfeld, 1915

(Pl. 5, Fig. 1, 2)

DESCRIPTION.—Hustedt 1928:438, fig. 239, 240.
ECOLOGY.—Polyhalobous, meioeuryhaline, subtropical to tropical seas (Pankow 1976); planktonic.
DISTRIBUTION.—Widespread in Sangamon and Recent sediments, not abundant. More common in Recent sediments from the entrapment zone in Suisun Bay.

REMARKS.—Several valves, which are identical to *C. jonesianus* in all respects except lacking the two prominent marginal processes, have been assigned to this species. They may represent a variety or one valve of a heterovalvar cell in which the other valve possesses those processes.

Coscinodiscus marginatus Ehrenberg, 1841

(Pl. 6, Fig. 6; Pl. 35, Fig. 4)

DESCRIPTION.—Hendey 1964:78, pl. 22, fig. 2.
ECOLOGY.—Oceanic plankton (Hendey 1964).
DISTRIBUTION.—Rare in Recent sediment.

Coscinodiscus nitidus Gregory, 1857

(Pl. 7, Fig. 3)

DESCRIPTION.—Hendey 1964:76, pl. 23, fig. 12.
ECOLOGY.—Polyhalobous, planktonic, meioeuryhaline (Pankow 1976).
DISTRIBUTION.—A single specimen from Recent sediment. Wong (1975) reported this species from plankton of central San Francisco Bay.

Coscinodiscus obscurus Schmidt, 1878

(Pl. 5, Fig. 6, 8–9; Pl. 6, Fig. 1)

DESCRIPTION.—Hustedt 1928:418, fig. 224.
ECOLOGY.—Planktonic, marine; pelagic in North Atlantic (Hustedt 1928).
DISTRIBUTION.—Widespread but not abundant in Sangamon and Recent sediment.

Coscinodiscus oculus-iridis Ehrenberg, 1839

(Pl. 5, Fig. 4)

DESCRIPTION.—Hendey 1964:78, pl. 24, fig. 1.
ECOLOGY.—Oceanic, planktonic (Hendey 1964).
DISTRIBUTION.—Present in Recent and Sangamon sediments.

REMARKS.—This species is similar to *C. asteromphalus* but is distinguished by fewer large areolae in the central rosette. *Coscinodiscus oculus-iridis* has five or fewer areolae in the central rosette (Hendey 1964), whereas *C. asteromphalus* has seven to nine (Brooks 1975). However, Brooks (1975:19) indicates that the central area of some specimens "have no large central rosette, the most central cribra being very little larger than the others." Therefore, the distinction between these two species may be tenuous.

Coscinodiscus radiatus Ehrenberg, 1839
(Pl. 5, Fig. 7; Pl. 6, Fig. 2–4)

DESCRIPTION.—Hustedt 1928:420, fig. 225.
ECOLOGY.—Polyhalobous, pleioeuryhaline (Pankow 1976), planktonic.
DISTRIBUTION.—Present in Recent and Sangamon sediment, rare.

Cyclotella Kutzing, 1833

Cyclotella comta (Ehrenberg) Kutzing, 1849
(Pl. 3, Fig. 3; Pl. 7, Fig. 7)

DESCRIPTION.—Hustedt 1928:354, fig. 183.
ECOLOGY.—Oligohalobous, meioeuryhaline (Pankow 1976).
DISTRIBUTION.—Rare in Recent and Sangamon sediments.

Cyclotella menegheniana Kutzing, 1844
(Pl. 3, Fig. 5)

DESCRIPTION.—Hustedt 1928:341, fig. 174.
ECOLOGY.—Oligohalobous, pleioeuryhaline, planktonic and benthic (Pankow 1976).
DISTRIBUTION.—Present in Recent sediments, most common in samples from Suisun and San Pablo bays.

Cyclotella pygmaea Pantocsek, 1892
(Pl. 3, Fig. 2; Pl. 7, Fig. 4)

DESCRIPTION.—Pantocsek 1892:37, 38, pl. 2, fig. 22; pl. 4, fig. 59.
ECOLOGY.—Fresh water (Schrader 1978).
DISTRIBUTION.—A single specimen from the Yerba Buena mud.

REMARKS.—This species has been reported only from fossil, freshwater material and this specimen is probably contamination from Plio-Pleistocene freshwater diatomites in northern California.

Cyclotella stelligera Cleve, 1881
(Pl. 3, Fig. 1)

DESCRIPTION.—Hustedt 1928:339, fig. 172.
ECOLOGY.—Fresh water.
DISTRIBUTION.—A single specimen from Recent sediments in San Pablo Bay.

Cyclotella striata (Kutzing) Grunow *in* Cleve and Grunow, 1880
(Pl. 3, Fig. 4, 6; Pl. 7, Fig. 5, 6)

DESCRIPTION.—Hustedt 1928:344, fig. 176.
ECOLOGY.—Marine to brackish water (Hendey 1964); a marine littoral species common in estuaries and inland salt water, a typical brackish-water diatom (Cholnoky 1968); meroplanktonic.
DISTRIBUTION.—Present but not abundant in Recent and Sangamon sediment.

Cyclotella stylorum Brightwell, 1860
(Pl. 3, Fig. 7–9)

DESCRIPTION.—Planktonic, marine (Hustedt 1928), meroplanktonic (Schuette and Schrader 1979).
DISTRIBUTION.—Abundant in Sangamon sediments, rare in Recent sediments.

REMARKS.—This is the most abundant species in the Yerba Buena mud. However its taxonomic status and ecology are unclear. Hustedt (1928) states that most authors would synonymize this species with *C. striata*. Hustedt retained *C. stylorum* based on the presence of marginal chambers on this species and their absence in *C. striata*. These species are very similar morphologically and are no doubt closely related. Schuette and Schrader (1979) considered *C. stylorum* and *C. striata* as a single taxonomic entity (their "*C. striata/stylorum*") for ecological purposes in a study of diatom taphocoenoses. Hasegawa (1975) reported *C. stylorum* from Pleistocene sediment on the west coast of Japan.

Cymatosira Grunow, 1862

Cymatosira belgica Grunow *in* Van Heurck, 1880–1885
(Pl. 15, Fig. 7–9, 13)

DESCRIPTION.—Hendey 1964:160. Hustedt 1931:127, fig. 649.
ECOLOGY.—Polyhalobous, meioeuryhaline, benthic (Pankow 1976); a common littoral species (Hendey 1964); probably tychopelagic.
DISTRIBUTION.—Abundant in Yerba Buena mud; present but not common in Recent sediments.

REMARKS.—This species is very abundant in Sangamon sediments from San Francisco Bay. From the work of Fryxell and Miller (1978) on *C. lorenziana*, it is inferred that *C. belgica* is a coastal marine species that forms chains attached to the substrate at one end. These chains are

occasionally torn from the substrate by currents or waves and live in the plankton.

Cymbella Agardh, 1830

Cymbella cistula (Ehrenberg *in* Hemprich and Ehrenberg, Kirchner *in* Cohn, 1878
(Pl. 28, Fig. 7)

DESCRIPTION.—Patrick and Reimer 1975:62, pl. 11, fig. 3, 4.
ECOLOGY.—Alkaliphilous, "indifferent" oligohalobous; eurytopic epiphyte (Patrick and Reimer 1966).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Cymbella meulleri var. *ventricosa* (Temperé and Peragallo) Reimer *in* Patrick and Reimer, 1975
(Pl. 28, Fig. 2)

DESCRIPTION.—Patrick and Reimer 1975:44, pl. 7, fig. 3a, 4.
ECOLOGY.—Poorly known.
DISTRIBUTION.—A single specimen from Recent sediment.

Cymbella mexicana (Ehrenberg) Cleve, 1894
(Pl. 28, Fig. 3–5)

DESCRIPTION.—Patrick and Reimer 1975:59, pl. 12, fig. 1, 2.
ECOLOGY.—Poorly known, fresh water.
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Cymbella mexicana var. *janischii* (Schmidt) Reimer *in* Patrick and Reimer 1975
(Pl. 28, Fig. 6)

DESCRIPTION.—Patrick and Reimer 1975:60, pl. 12, fig. 3a, b.
ECOLOGY.—Not known, probably fresh water.
DISTRIBUTION.—A single specimen from sediment in Suisun Bay.

Cymbella minuta Hilse *in* Rabenhorst, 1861–1879
(Pl. 27, Fig. 14)

DESCRIPTION.—Patrick and Reimer 1975:47, pl. 8, fig. 1–4b.
ECOLOGY.—Eurytopic, oligohalobous (Patrick and Reimer 1975).
DISTRIBUTION.—Rare in Sangamon sediment.

Cymbella prostrata (Berk.) Cleve, 1894
(Pl. 27, Fig. 12)

DESCRIPTION.—Patrick and Reimer 1975:40, pl. 6, fig. 4.
ECOLOGY.—Alkaliphilous, indifferent oligohalobous (Pankow 1976).
DISTRIBUTION.—Rare in Recent and Sangamon sediment.

Cymbella prostrata var. *auerswaldii* (Rabenhorst) Reimer *in* Patrick and Reimer, 1975
(Pl. 27, Fig. 15)

DESCRIPTION.—Patrick and Reimer 1975:41, pl. 6, fig. 5, 6.
ECOLOGY.—Insufficiently known.
DISTRIBUTION.—A single specimen from Sangamon sediments.

Cymbella sinuata Gregory, 1856
(Pl. 27, Fig. 13)

DESCRIPTION.—Patrick and Reimer 1975:51, pl. 9, fig. 3, 4.
ECOLOGY.—Oligohalobous (Patrick and Reimer 1975).
DISTRIBUTION.—Rare in Recent sediment.

Cymbella triangulum (Ehrenberg) Cleve, 1894
(Pl. 27, Fig. 12; Pl. 28, Fig. 1)

DESCRIPTION.—Patrick and Reimer 1975:45, pl. 7, fig. 7–10.
ECOLOGY.—A fresh-water species, alkaliphilous.
DISTRIBUTION.—Rare in Recent and Sangamon sediments.

Cymbella tumidula Grunow *in* Schmidt, 1875
(No illustration)

DESCRIPTION.—Patrick and Reimer 1975:56, pl. 10, fig. 6.
ECOLOGY.—Fresh water, alkaliphilous (Patrick and Reimer 1975).
DISTRIBUTION.—Rare in sediment from San Pablo and Suisun Bays.

Denticula Kutzing, 1844

Denticula subtilis Grunow, 1862
(Pl. 30, Fig. 12, 13)

DESCRIPTION.—Patrick and Reimer 1975:172, pl. 22, fig. 10, 11.
ECOLOGY.—A brackish-water, estuarine species (Patrick and Reimer 1975).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Denticula thermalis Kutzing, 1844
(No illustration)

DESCRIPTION.—Patrick and Reimer 1975:174, pl. 22, fig. 18, 19.
ECOLOGY.—A fresh-water species.
DISTRIBUTION.—A single specimen from Sangamon sediment.

Diatoma Bory, 1824

Diatoma anceps (Ehrenberg *in* Hemprich and Ehrenberg) Kirchner *in* Cohn, 1878
(Pl. 15, Fig. 12)

DESCRIPTION.—Patrick and Reimer 1966:106, pl. 2, fig. 1–3.
ECOLOGY.—Fresh water.
DISTRIBUTION.—A single specimen from the Yerba Buena mud.

Diatoma vulgare var. *breve* Grunow, 1862
(Pl. 15, Fig. 11)

DESCRIPTION.—Patrick and Reimer 1966:110, pl. 2, fig. 10, 11.

ECOLOGY.—Prefers cool, fresh water (Patrick and Reimer 1966).

DISTRIBUTION.—A single specimen from Recent sediments.

Dimeregramma Ralfs *in* Pritchard, 1861

Dimeregramma minor (Gregory) Ralfs *in* Pritchard, 1861

(Pl. 15, Fig. 15, 16)

DESCRIPTION.—Hendey 1964:156, Pl. 27, Fig. 12.

ECOLOGY.—Polyhalobous, mesoeuryhaline, epiphytic on macroalgae (Pankow 1976).

DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Diploneis Ehrenberg, 1844

Diploneis bombus Ehrenberg, 1844

(Pl. 23, Fig. 3)

DESCRIPTION.—Hendey 1964:227, pl. 32, fig. 2. Hustedt 1937: 704, fig. 1086.

ECOLOGY.—Polyhalobous, meio- to mesoeuryhaline (Pankow 1976); brackish-water species, benthic (Hendey 1964).

DISTRIBUTION.—Rare but widespread in Sangamon and Recent sediments.

Diploneis decipiens Cleve-Euler, 1915

(Pl. 23, Fig. 5)

DESCRIPTION.—Cleve-Euler 1953:77, fig. 645.

ECOLOGY.—Marine and brackish water.

DISTRIBUTION.—Abundant in sediments from Suisun Bay.

REMARKS.—The identification of this species is uncertain. The specimens from this study are smaller (length is 9–20 μm, width is 5–11 μm) than the description given by Cleve-Euler. However, the number of striae (9–12 in 10 μm) agrees with Cleve-Euler's description as do the other aspects of morphology. The specimens in this study are similar to *D. puella* (Schum.) Cl. described by Patrick and Reimer (1966) and Germain (1979), but the striae are coarser.

Diploneis interrupta (Kutzing) Cleve, 1894

(Pl. 23, Fig. 1, 2)

DESCRIPTION.—Hustedt 1937:602, fig. 1019. Patrick and Reimer 1966:416, pl. 38, fig. 12.

ECOLOGY.—Mesohalobous (Pankow 1976), brackish water, benthic.

DISTRIBUTION.—Rare in Sangamon and Recent sediment.

Diploneis oblongella (Naeg. *in* Kutzing) Ross, 1947

(Pl. 22, Fig. 15, 16)

DESCRIPTION.—Patrick and Reimer 1966:413, pl. 38, fig. 8.

ECOLOGY.—Oligohalobous, mesoeuryhaline, benthic (Pankow 1976); fresh to slightly brackish water (Patrick and Reimer 1966).

DISTRIBUTION.—Widespread but rare in San Pablo and Suisun Bay samples, Recent.

REMARKS.—Patrick and Reimer (1966) consider *D. ovalis*, a more commonly known species, synonymous with *D. oblongella*. The epithet *oblongella* has priority. Hustedt (1937) considered *D. oblongella* a variety of *D. ovalis*.

Diploneis papula var. *constricta* Hustedt, 1937

(Pl. 23, Fig. 6)

DESCRIPTION.—Hustedt 1937:679, 680, fig. 1071d.

ECOLOGY.—Benthic, warm, coastal marine waters.

DISTRIBUTION.—Rare in Sangamon sediments.

Diploneis smithii (Brébisson *in* Smith) Cleve, 1894

(Pl. 22, Fig. 7, 12, 13)

DESCRIPTION.—Hustedt 1937:647, fig. 1051, 1052. Patrick and Reimer 1966:410, pl. 38, fig. 2–4.

ECOLOGY.—Polyhalobous, plioeuryhaline, benthic (Pankow 1976); in slightly brackish to brackish water (Patrick and Reimer 1966).

DISTRIBUTION.—Present in Sangamon and Recent sediments.

REMARKS.—This is the most abundant species of *Diploneis* and no doubt several of the commonly recognized varieties are present (see Pl. 22). No attempt was made to consistently distinguish the varieties because they are not sufficiently common.

Diploneis sp. 6

(Pl. 23, Fig. 4)

DESCRIPTION.—Valve linear-elliptical. Longitudinal canal indistinct. Axial area lanceolate, central area rectangular, wider than long. Costae and striae moderately radiate, punctae indistinct. Striae, 15–17 μm; length, 25 μm; breadth, 12 μm.

DISTRIBUTION.—A single specimen from Sangamon sediments.

REMARKS.—This specimen is similar to *D. oculata* (Brébisson) Cleve except that the striae are coarser and more radiate.

Ditylum Bailey, 1861

Ditylum brightwellii (West) Grunow *in* Van Heurck, 1880–1885

(Pl. 15, Fig. 5, 6)

DESCRIPTION.—Hendey 1964:111, pl. 5, fig. 1.

ECOLOGY.—Polyhalobous, meioeuryhaline (Pankow 1976); planktonic, neritic species (Hendey 1964).

DISTRIBUTION.—A common and widespread species in San-

gamon and Recent sediment. Typically the corona and central spine are preserved; rarely is the entire valve present.

Entomoneis Ehrenberg, 1845

Entomoneis alata (Ehrenberg) Ehrenberg, 1845
(Pl. 27, Fig. 1)

DESCRIPTION.—Patrick and Reimer 1975:3, pl. 1, fig. 2.
ECOLOGY.—Benthic, mesohalobous (Pankow 1976), marine (Cholnoky 1968), marine to brackish.
DISTRIBUTION.—Intertidal mud flats, Recent sediments, not common.

Entomoneis paludosa (Smith) Reimer *in* Patrick and Reimer, 1975
(Pl. 26, Fig. 10)

DESCRIPTION.—Patrick and Reimer 1975:4, pl. 1, fig. 1.
ECOLOGY.—Mesohalobous euryhaline (Pankow 1976); fresh to moderately brackish water, benthic.
DISTRIBUTION.—Intertidal areas of Recent bay.

Entomoneis sp. 1
(Pl. 26, Fig. 11)

DESCRIPTION.—Valve aspect lanceolate to linear-lanceolate with acute apices. Valve surface with transverse striae, striae doubly punctate. Raphe canal sigmoid, crossed by costae which form a fibulate appearance like that in the genus *Nitzschia*. Length is 105 μm, width is 10 μm, striae 7–8 in 10 μm.
DISTRIBUTION.—A single specimen from Recent intertidal salt marsh sediments, Albany mud flats.

REMARKS.—This species is very similar to *E. conspicua* Greville and *E. pulchra* (Bailey) Reimer (see Hustedt 1955:37; Patrick and Reimer 1975:5). The girdle aspect was not observed therefore this specimen could not be positively assigned to either of those closely related species.

Epithemia Brébisson, 1838

Epithemia adnata var. *porcellus* (Kutzing) Patrick *in* Patrick and Reimer, 1975
(Pl. 30, Fig. 5)

DESCRIPTION.—Patrick and Reimer 1975:180, pl. 24, fig. 6.
ECOLOGY.—Oligohalobous (indifferent), mesoeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—A single specimen from Sangamon sediments.

Epithemia argus (Ehrenberg) Kutzing, 1844
(Pl. 30, Fig. 3)

DESCRIPTION.—Patrick and Reimer 1975:175, pl. 23, fig. 1. Hustedt 1930*b*:384, fig. 727b.
ECOLOGY.—Oligohalobous (indifferent), meioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—A single specimen from Sangmon sediments.

Epithemia sorex Kutzing, 1844
(Pl. 30, Fig. 4)

DESCRIPTION.—Patrick and Reimer 1975:188, pl. 27, fig. 4.
ECOLOGY.—Oligohalobous (indifferent), pleioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Epithemia turgida (Ehrenberg) Kutzing, 1844
(Pl. 30, Fig. 1)

DESCRIPTION.—Patrick and Reimer 1975:182, pl. 25, fig. 1a, b.
ECOLOGY.—Oligohalobous (indifferent), pleioeuryhaline, upper limit 17‰ (Pankow 1976).
DISTRIBUTION.—Frequent and widespread in Sangamon and Recent sediments.

Epithemia turgida var. *westermanii* (Ehrenberg) Grunow, 1862
(Pl. 30, Fig. 2)

DESCRIPTION.—Patrick and Reimer 1975:184, pl. 25, fig. 2. Cleve-Euler 1952:40, fig. 1410n, o.
ECOLOGY.—Fresh water (Patrick and Reimer 1966).
DISTRIBUTION.—Rare in Sangamon and Recent sediment.

Eunotia Ehrenberg, 1837

Eunotia arcus Ehrenberg, 1837
(Pl. 17, Fig. 4)

DESCRIPTION.—Patrick and Reimer 1966:212, pl. 13, fig. 11.
ECOLOGY.—Fresh water (Patrick and Reimer 1966).
DISTRIBUTION.—A single specimen from Sangamon sediment.

Eunotia arcus var. *bidens* (Ehrenberg) Grunow, 1881
(Pl. 17, Fig. 6)

DESCRIPTION.—Patrick and Reimer 1966:213, pl. 13, fig. 12.
ECOLOGY.—Fresh, slightly acid water.
DISTRIBUTION.—A single specimen from Sangamon sediments.

Eunotia eruca Ehrenberg, 1854
(Pl. 17, Fig. 1–3)

DESCRIPTION.—Patrick and Reimer 1966:161, pl. 9, fig. 8, 9, as "Amphicampa mirabilis" (Reaside 1970:537).
ECOLOGY.—Fresh water, benthic, tolerates slightly brackish water (Reaside 1970).
DISTRIBUTION.—Rare in the Yerba Buena mud.

Eunotia monodon Ehrenberg, 1843
(Pl. 17, Fig. 5, 7)

DESCRIPTION.—Patrick and Reimer 1966:198, pl. 11, fig. 6.
ECOLOGY.—Fresh water, in cool- to cold-water swamps (Patrick and Reimer 1966).
DISTRIBUTION.—Rare but widespread in Sangamon and Recent sediment.

Eunotia triodon Ehrenberg, 1837
(Pl. 17, Fig. 8)

DESCRIPTION.—Patrick and Reimer 1966:200, pl. 12, fig. 1.
ECOLOGY.—Oligotrophic, slightly acid water.
DISTRIBUTION.—A single specimen from Sangamon sediments.

Eunotogramma Weisse, 1854

Eunotogramma marinum (Smith) Peragallo and Peragallo, 1897–1908
(Pl. 15, Fig. 10)

DESCRIPTION.—Hustedt 1955:10, pl. 4, fig. 10–17.
ECOLOGY.—A marine and brackish-water species.
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Fragilaria Lyngbye, 1819

Fragilaria brevistriata Grunow *in* Van Heurck, 1880–1885
(Pl. 16, Fig. 23)

DESCRIPTION.—Patrick and Reimer 1966:128, pl. 4, fig. 14.
ECOLOGY.—Oligohalobous, mesoeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Rare in sediments from San Pablo and Suisun Bays.

Fragilaria capucina Desmazieres, 1825
(Pl. 16, Fig. 14)

DESCRIPTION.—Patrick and Reimer 1966:118, pl. 13, fig. 5. Lange-Bertalot 1980*b*, fig. 39–81, 239–242.
ECOLOGY.—"Indifferent" oligohalobous.
DISTRIBUTION.—Rare in Recent sediments.

Fragilaria capucina var. *vaucheriae* (Kutzing) Lange-Bertalot, 1980*b*
(Pl. 16, Fig. 25)

DESCRIPTION.—Patrick and Reimer 1966:120, pl. 3, as *F. vaucheriae*. Lange-Bertalot 1980*b*, fig. 26–38, 216–235.
ECOLOGY.—A fresh-water species.
DISTRIBUTION.—Rare in Recent sediments.

Fragilaria construens (Ehrenberg) Grunow, 1862
(Pl. 16, Fig. 20)

DESCRIPTION.—Patrick and Reimer 1966:125, pl. 4, fig. 4.
ECOLOGY.—Oligohalobous, meio- to mesoeuryhaline, benthic? (Pankow 1976).
DISTRIBUTION.—Rare but widespread in Recent and Sangamon sediments.

Fragilaria construens var. *binodis* (Ehrenberg) Grunow, 1862
(Pl. 16, Fig. 18)

DESCRIPTION.—Patrick and Reimer 1966:125, pl. 4, fig. 7.
ECOLOGY.—Same as species.
DISTRIBUTION.—Same as species.

Fragilaria construens var. *pumila* Grunow, 1881
(Pl. 16, Fig. 22)

DESCRIPTION.—Patrick and Reimer 1966:126, pl. 4, fig. 5, 6.
ECOLOGY.—Same as species.
DISTRIBUTION.—Frequent in San Pablo and Suisun Bays.

Fragilaria construens var. *venter* (Ehrenberg) Grunow, 1881
(Pl. 16, Fig. 12)

DESCRIPTION.—Patrick and Reimer 1966:126, pl. 4, fig. 8, 9.
ECOLOGY.—Same as species.
DISTRIBUTION.—Widespread and frequent in Sangamon and Recent sediments.

Fragilaria crotonensis Kitton, 1869
(Pl. 16, Fig. 15)

DESCRIPTION.—Patrick and Reimer 1966:121, pl. 3, fig. 11, 12.
ECOLOGY.—Oligohalobous, meioeuryhaline (Pankow 1976).
DISTRIBUTION.—A single specimen from Sangamon sediments.

Fragilaria lapponica Grunow, 1881
(Pl. 16, Fig. 21)

DESCRIPTION.—Patrick and Reimer 1966:130, pl. 4, fig. 17.
ECOLOGY.—Fresh water, tolerates low salt concentrations (Patrick and Reimer 1966).
DISTRIBUTION.—Rare in Sangamon sediments.

Fragilaria leptostauron (Ehrenberg) Hustedt, 1931
(Pl. 16, Fig. 24)

DESCRIPTION.—Patrick and Reimer 1966:124, pl. 4, fig. 2.
ECOLOGY.—"Indifferent" oligohalobous, mesoeuryhaline (Pankow 1976).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Fragilaria tabulata (Agardh) Lange-Bertalot, 1980*b*
(Pl. 16, Fig. 13)

DESCRIPTION.—Patrick and Reimer 1966:141, pl. 5, fig. 17, 18. Lange-Bertalot 1980*b*, fig. 155–173, 268–278.
ECOLOGY.—Mesohalobous, euryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Frequent and widely distributed in Sangamon and Recent sediment.

REMARKS.—Patrick and Reimer (1966:141) indicate that the correct epithet for this taxon is *fasciculata* (*Synedra fasciculata*). Lange-Bertalot (1980*b*:749) noted this priority, but maintained the epithet *tabulata* because of its widespread usage in the modern literature.

Fragilaria ulna (Nitzsch) Lange-Bertalot, 1980*b*
(Pl. 16, Fig. 16, 17)

DESCRIPTION.—Patrick and Reimer 1966:148, pl. 7, fig. 1, 2. Lange-Bertalot 1980*b*, fig. 174–197, 258–267.
ECOLOGY.—Oligohalobous, mesoeuryhaline (Pankow 1976).
DISTRIBUTION.—Widespread in Sangamon and Recent sediments.

Fragilaria virescens var. *elliptica* Hustedt, 1914
(Pl. 16, Fig. 19)

DESCRIPTION.—Hustedt 1931:163, fig. 672a, e.
ECOLOGY.—Fresh water (Hustedt 1931).
DISTRIBUTION.—A single specimen from San Pablo Bay.

Frustulia Rabenborst, 1853

Frustulia asymmetrica (Cl.) Hustedt, 1954
(Pl. 19, Fig. 13)

DESCRIPTION.—Patrick and Reimer 1966:305, pl. 22, fig. 4.
ECOLOGY.—Mesohalobous (Patrick and Reimer 1966).
DISTRIBUTION.—Intertidal mud-flat and salt-marsh sediments of present bay.

Frustulia interposita (Lewis) Cleve, 1894*b*
(Pl. 19, Fig. 14)

DESCRIPTION.—Patrick and Reimer 1966:305, pl. 22, fig. 5.
ECOLOGY.—Fresh water (Patrick and Reimer 1966).
DISTRIBUTION.—A single specimen from Sangamon sediments.

Gomphoneis Cleve, 1894

Gomphoneis eriense (Grunow) Skvortzow and Meyer, 1928
(Pl. 29, Fig. 11)

DESCRIPTION.—Patrick and Reimer 1975:148, pl. 20, fig. 3.
ECOLOGY.—A cool, fresh-water species.
DISTRIBUTION.—A single specimen form Sangamon sediments.

Gomphoneis herculeana (Ehrenberg) Cleve, 1894
(Pl. 29, Fig. 12)

DESCRIPTION.—Patrick and Reimer 1975:149, pl. 21, fig. 1.
ECOLOGY.—Prefers fresh, cool water (Patrick and Reimer 1975).
DISTRIBUTION.—Rare in Sangamon and Recent sediment, most abundant in Suisun Bay sediments.

Gomphonema Ehrenberg, 1832 *nom. cons. non* Agardh

Gomphonema affine Kutzing, 1844
(Pl. 29, Fig. 10)

DESCRIPTION.—Patrick and Reimer 1975:133, pl. 17, fig. 5.
ECOLOGY.—Fresh water.
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Gomphonema angustatum var. *sarcophagus* (Gregory) Grunow, 1880
(Pl. 29, Fig. 5, 6)

DESCRIPTION.—Patrick and Reimer 1975:128, pl. 17, fig. 23.
ECOLOGY.—In fresh, mesotropic water (Patrick and Reimer 1966).
DISTRIBUTION.—Rare in Recent sediments from San Pablo Bay.

REMARKS.—Patrick and Reimer (1975) give measurements of 7–11 striae in 10 μm. The specimen figured here has 6 striae in 10 μm.

Gomphonema apicatum Ehrenberg, 1854
(No illustration)

DESCRIPTION.—Patrick and Reimer 1975:110, pl. 15, fig. 1.
ECOLOGY.—Poorly known.
DISTRIBUTION.—A single specimen from Sangamon sediment.

Gomphonema gracile (Ehrenberg) emend. Van Heurck, 1885
(Pl. 29, Fig. 4)

DESCRIPTION.—Patrick and Reimer 1975:131, pl. 17, fig. 1–3.
ECOLOGY.—"Indifferent" oligohalobous, benthic and planktonic (Patrick and Reimer 1975).
DISTRIBUTION.—Rare in Sangamon sediment.

Gomphonema grovei Schmidt, 1899
(Pl. 29, Fig. 3)

DESCRIPTION.—Patrick and Reimer 1975:142, pl. 18, fig. 24a, b.
ECOLOGY.—Oligohalobous (Patrick and Reimer 1975).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Gomphonema parvulum (Kutzing) Kutzing, 1849
(Pl. 29, Fig. 7)

DESCRIPTION.—Patrick and Reimer 1975:122, pl. 17, fig. 7–12.
ECOLOGY.—Fresh water.
DISTRIBUTION.—A single specimen from Recent sediment in San Pablo Bay.

Gomphonema rhombicum Fricke, 1904
(Pl. 29, Fig. 8)

DESCRIPTION.—Carter 1970:616, pl. 4, fig. 6.
ECOLOGY.—Fresh water, benthic.
DISTRIBUTION.—A single specimen from Recent sediment.

Gomphonema septum Moghadam, 1969
(Pl. 29, Fig. 9)

DESCRIPTION.—Patrick and Reimer 1975:136, pl. 19, fig. 1.
ECOLOGY.—Cool, circumneutral fresh water (Patrick and Reimer 1975).

DISTRIBUTION.—A single specimen from the Yerba Buena mud.

Gomphonema ventricosum Gregory, 1856

(Pl. 29, Fig. 1, 2)

DESCRIPTION.—Patrick and Reimer 1975:137, pl. 19, fig. 2.
ECOLOGY.—Cool, fresh water (Patrick and Reimer 1975).
DISTRIBUTION.—Rare in Sangamon sediment.

Grammatophora Ehrenberg, 1840

Grammatophora marina (Lyngbye) Kutzing, 1844

(Pl. 15, Fig. 14, 17, 18)

DESCRIPTION.—Hendey 1964:170. Hustedt 1931:43, fig. 569, 570.
ECOLOGY.—Polyhalobous, meso- to meioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Widespread but not abundant in Sangamon and Recent sediments; common in a few samples from Yerba Buena mud.

Gyrosigma Hassall, 1845

Gyrosigma acuminatum (Kutzing) Rabenhorst, 1853

(Pl. 20, Fig. 3, 4)

DESCRIPTION.—Patrick and Reimer 1966:314, pl. 23, fig. 1–3.
ECOLOGY.—"Indifferent" oligohalobous, mesoeuryhaline, in inland salt waters (Pankow 1976); can withstand slightly salty waters.
DISTRIBUTION.—Common in intertidal salt-marsh and mudflat samples near stream mouth.

REMARKS.—These specimens show the dimensions and shape of *G. acuminatum* but have a pattern of striae similar to *G. attenuatum.*

Gyrosigma balticum (Ehrenberg) Rabenhorst, 1853

(Pl. 20, Fig. 5)

DESCRIPTION.—Patrick and Reimer 1966:324, pl. 25, fig. 1.
ECOLOGY.—Mesohalobous, euryhaline benthic (Pankow 1976); a marine littoral species often in brackish, estuarine waters (Hendey 1964).
DISTRIBUTION.—Frequent and widespread in Sangamon and Recent sediments; most abundant on intertidal mud flats and salt marshes in present bay.

Gyrosigma exile (Grunow) Reimer *in* Patrick and Reimer, 1966

(Pl. 19, Fig. 12; Pl. 20, Fig. 1)

DESCRIPTION.—Patrick and Reimer 1966:322, pl. 24, fig. 4.
ECOLOGY.—Fresh to slightly brackish water, "indifferent" oligohalobous (Patrick and Reimer 1966).
DISTRIBUTION.—Intertidal mud flats and marshes in present bay.

Gyrosigma eximium (Thwaites) Boyer, 1927

(Pl. 19, Fig. 10, 11)

DESCRIPTION.—Patrick and Reimer 1966:317, pl. 23, fig. 6.
ECOLOGY.—Characteristic of brackish water, but also in fresh water (Patrick and Reimer 1966).
DISTRIBUTION.—Intertidal mud flats and marshes in present bay.

Gyrosigma fasciola (Ehrenberg) Griffith and Henfrey, 1856

(Pl. 20, Fig. 2)

DESCRIPTION.—Patrick and Reimer 1966:328, pl. 26, fig. 4.
ECOLOGY.—Mesohalobous, benthic (Pankow 1976); brackish to marine salinities 1–20‰ (Patrick and Reimer 1966).
DISTRIBUTION.—Common and widespread in Recent sediment from central and southern San Francisco Bay.

Hantzschia Grunow *in* Cleve and Grunow, 1880

Hantzschia amphioxys (Ehrenberg) Grunow, 1880

(Pl. 31, Fig. 3)

DESCRIPTION.—Hustedt 1930*b*:394, fig. 747–750. Cleve-Euler 1952:46, fig. 1419–1421.
ECOLOGY.—In fresh to slightly brackish water, aerophilic (Cleve-Euler 1952).
DISTRIBUTION.—Rare but widespread in Sangamon and Recent sediment.

Hyalodiscus Ehrenberg, 1845

Hyalodiscus scoticus (Kutzing) Grunow, 1879

(Pl. 12, Fig. 10, 11)

DESCRIPTION.—Hendey 1964:90. Hustedt 1928:293, fig. 133.
ECOLOGY.—Mesohalobous (Pankow 1976).
DISTRIBUTION.—Rare in Sangamon and Recent sediment.

Hydrosera Wallich, 1858

Hydrosera triquetra Wallich, 1858

(Pl. 14, Fig. 3)

DESCRIPTION.—Frenguelli 1953:73–75, pl. 3, fig. 4.
ECOLOGY.—A brackish-water species from Recent sediments.
DISTRIBUTION.—A single specimen from Recent sediments.

Isthmia Agardh, 1832

Isthmia nervosa Kutzing, 1844

(Pl. 14, Fig. 4)

DESCRIPTION.—Hustedt 1930*a*:865, fig. 515.

ECOLOGY.—A littoral, marine species; epiphytic (Hustedt 1930*b*).

DISTRIBUTION.—Rare in Sangamon and Recent sediments.

REMARKS.—This large species is common along the northern California coast. Sloan (1981) reported abundant *I. nervosa* in some samples from the Yerba Buena mud. That data was taken from sieved samples and is difficult to compare with the occurrence found in whole sample mounts.

Mastogloia Thwaites *in* Smith, 1856

Mastogloia exigua Lewis, 1862

(Pl. 19, Fig. 8, 9)

DESCRIPTION.—Hustedt 1933:569, fig. 1003.

ECOLOGY.—Mesohalobous; widespread in coastal waters (Pankow 1976).

DISTRIBUTION.—Intertidal mud flat and marshes of present bay.

Melosira Agardh, 1824

Melosira arenaria Moore, 1843

(Pl. 2, Fig. 1)

DESCRIPTION.—Hustedt 1927:269, fig. 114.

ECOLOGY.—A littoral marine species (Hustedt 1927).

DISTRIBUTION.—A single specimen from Sangamon sediment.

Melosira moniliformis (O. F. Muller) Agardh, 1824

(Pl. 1, Fig. 1–6)

DESCRIPTION.—Crawford 1977:277–285.

ECOLOGY.—Polyhalobous, pleioeuryhaline, benthic, and planktonic (Pankow 1976).

DISTRIBUTION.—Widely distributed in Sangamon and Recent sediments, abundant in samples from Albany mud flats.

Melosira nummuloides (Dillw.) Agardh, 1824

(Pl. 1, Fig. 7)

DESCRIPTION.—Crawford 1975:323–338.

ECOLOGY.—Mesohalobous (Pankow 1976).

DISTRIBUTION.—Widespread in Recent sediment, abundant in Albany mud flats.

Meridion Agardh, 1824

Meridion circulare var. *constrictum* (Ralfs) Van Heurck, 1885

(Pl. 16, Fig. 4)

DESCRIPTION.—Patrick and Reimer 1966:114, pl. 2, fig. 16.

ECOLOGY.—Fresh to slightly brackish water.

DISTRIBUTION.—A single specimen from the Yerba Buena mud.

Navicula Bory, 1824

Navicula abunda Hustedt, 1955

(Pl. 23, Fig. 13)

DESCRIPTION.—Hustedt 1955:27, pl. 9, fig. 10–12.

ECOLOGY.—Marine to brackish water? (Hustedt 1955).

DISTRIBUTION.—A single specimen in Recent sediments from Albany mud flats.

Navicula auriculata Hustedt, 1944

(Pl. 25, Fig. 7)

DESCRIPTION.—Patrick and Reimer 1966:441, pl. 39, fig. 1.

ECOLOGY.—Poorly known.

DISTRIBUTION.—Recent intertidal mud-flat and salt-marsh sediments, not common.

Navicula aurora Sovereign, 1958

(Pl. 23, Fig. 10)

DESCRIPTION.—Patrick and Reimer 1966:532, pl. 51, fig. 3, 4.

ECOLOGY.—Fresh water.

DISTRIBUTION.—A single specimen from the Yerba Buena mud.

Navicula circumtexta Meister *in* Hustedt, 1934

(Pl. 23, Fig. 7, 8)

DESCRIPTION.—Patrick and Reimer 1966:442, pl. 39, fig. 3.

ECOLOGY.—Prefers fresh, hard water (Patrick and Reimer 1966).

DISTRIBUTION.—Frequent in Recent sediments from Albany mud flats and salt marsh; epiphytic on microalgae.

Navicula cryptocephala Kutzing, 1844

(Pl. 23, Fig. 9)

DESCRIPTION.—Patrick and Reimer 1966:503, pl. 48, fig. 3.

ECOLOGY.—Fresh to slightly brackish water; oligohalobous "indifferent," pleio- or more likely holoeuryhaline (Pankow 1976).

DISTRIBUTION.—Common only in intertidal mud flats and marsh sediments of present bay, Albany mud flats.

REMARKS.—This assignment is somewhat doubtful. The shape, dimensions, and striae of these specimens agree well with published descriptions of *N. cryptocephala,* but the central area of these specimens is indistinct and uncharacteristic of *N. cryptocephala.*

Navicula cuspidata (Kutzing) Kutzing, 1844

(Pl. 23, Fig. 11, 12)

DESCRIPTION.—Patrick and Reimer 1966:464, pl. 43, fig. 9, 10.

ECOLOGY.—"Indifferent," oligohalobous (Pankow 1976).

DISTRIBUTION.—Rare in Recent sediments.

Navicula digito-radiata (Gregory) Ralfs *in* Pritchard, 1861
(Pl. 23, Fig. 16)

DESCRIPTION.—Hendey 1964:202, pl. 29, fig. 8, 9.
ECOLOGY.—Mesohalobous (Pankow 1976), common on muddy shores (Hendey 1964).
DISTRIBUTION.—Frequent in Recent sediments from intertidal mud flats and marshes.

Navicula distans (Smith) Ralfs *in* Pritchard, 1861
(Pl. 23, Fig. 17)

DESCRIPTION.—Hendey 1964:203, pl. 27, fig. 13.
ECOLOGY.—Marine to brackish water, benthic (Hendey 1964).
DISTRIBUTION.—Rare, but widespread in Sangamon and Recent sediments.

Navicula elegans Smith, 1853
(No illustration)

DESCRIPTION.—Patrick and Reimer 1966:540, pl. 52, fig. 8, 9.
ECOLOGY.—Fresh to brackish water, benthic.
DISTRIBUTION.—Intertidal mud flats and salt marshes of present bay.

Navicula elginensis (Gregory) Ralfs *in* Pritchard, 1861
(Pl. 24, Fig. 3)

DESCRIPTION.—Patrick and Reimer 1966:524, pl. 50, fig. 3.
ECOLOGY.—Fresh to slightly brackish water; oligohalobous "indifferent," mesoeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Rare in Recent sediments from San Pablo Bay.

Navicula expansa Hagelstein, 1939
(Pl. 25, Fig. 2)

DESCRIPTION.—Patrick and Reimer 1966:459, pl. 43, fig. 1–3.
ECOLOGY.—Brackish water; common in tropical swamps (Hendey 1964).
DISTRIBUTION.—A single specimen from the Recent sediments of Albany mud flats.

Navicula granulata Bailey, 1853
(Pl. 24, Fig. 2)

DESCRIPTION.—Hendey 1964:208, pl. 31, fig. 6
ECOLOGY.—Polyhalobous, meioeuryhaline, littoral, benthic (Pankow 1976).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

REMARKS.—Despite the work of Hendey (1953), much disagreement still remains as to the status of *N. granulata* Bailey, *N. brasiliensis* Grunow, *N. marina* Ralfs, and *N. punctulata* Smith (compare Hendey 1951, 1953, 1958, 1964, 1970; Hustedt 1955, 1961; and Patrick and Reimer 1966). Most workers agree that these species are closely related and in some cases synonymous. It appears from inspection of the literature that each species has a restricted geographical and ecological distribution (see Hendey 1970). The "species" may represent geographical and ecological variants of a single taxon. Culture studies might shed light on this problem. I distinguish the various morphs as separate species to be consistent with previous work, although some intergradation is apparent (see *N. punctulata*).

Navicula gregaria Donkin, 1861
(Pl. 24, Fig. 4, 5, 9–11)

DESCRIPTION.—Patrick and Reimer 1966:467, pl. 44, fig. 6.
ECOLOGY.—Mesohalobous, benthic, "prefers brackish water and fresh water with high mineral content." (Patrick and Reimer 1966:468).
DISTRIBUTION.—Intertidal salt-marsh sediments of present bay, Albany mud flats.

Navicula humii Hustedt, 1955
(Pl. 24, Fig. 12)

DESCRIPTION.—Hustedt 1955:23, pl. 8, fig. 8–10, 24.
ECOLOGY.—Poorly known, previously only reported from the type area.
DISTRIBUTION.—A single specimen from Sangamon sediment.

Navicula mutica Kutzing, 1844
(Pl. 24, Fig. 13, 14)

DESCRIPTION.—Patrick and Reimer 1966:454, pl. 42, fig. 2.
ECOLOGY.—Oligohalobous "indifferent," meso- to pleioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Rare but widespread in Sangamon and Recent sediments.

Navicula peregrina (Ehrenberg) Kutzing, 1844
(Pl. 24, Fig. 19, 20)

DESCRIPTION.—Patrick and Reimer 1966:533, pl. 51, fig. 5. Hendey 1964:201, pl. 30, fig. 12, 13.
ECOLOGY.—Prefers brackish water; mesohalobous, euryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Common in sediments from Recent intertidal mud flats and salt marshes.

Navicula pseudolanceolata Lange-Bertalot, 1980*a*
(Pl. 25, Fig. 6)

DESCRIPTION.—Lange-Bertalot 1980*a*:32, pl. 2, fig. 1–8.
ECOLOGY.—Probably mesohalobous, widely distributed.
DISTRIBUTION.—Rare in Recent and Sangamon sediments.

REMARKS.—Lange-Bertalot (1980*a*) recently revised the "Navicula lineolatae" Cl. which includes *N. lanceolata, N. trivialis, N. pseudolan-*

ceolata, and several other species. The subtle distinctions between the species are difficult to evaluate without comparative material. The specimens from San Francisco Bay best fit the description of *N. pseudolanceolata,* but this assignment is questionable.

Navicula punctulata Smith, 1853

(Pl. 24, Fig. 1)

DESCRIPTION.—Patrick and Reimer 1966:499, pl. 41, fig. 1.
ECOLOGY.—Polyhalobous, meioeuryhaline, benthic (Pankow 1976 for *N. marina*); a brackish-water species (Patrick and Reimer 1966).
DISTRIBUTION.—Rare in Sangamon sediments.

REMARKS.—Patrick and Reimer (1966) synonymized *N. marina* Ralfs (1861) with *N. punctulata* based on their morphological similarity and the priority of Wm. Smith's epithet. In contrast, Hustedt (1966) and Hendey (1964) took *N. marina* Ralfs (1861) as the correct epithet and synonymized *punctulata.* The two taxa are apparently conspecific and *punctulata* is the valid epithet based on the rules of priority.

Navicula pusilla Smith, 1853

(Pl. 24, Fig. 16)

DESCRIPTION.—Patrick and Reimer 1966:452, pl. 41, fig. 7.
ECOLOGY.—Fresh to slightly brackish water; oligohalobous "indifferent," mesoeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—A single specimen in Sangamon sediment.

Navicula pusilla var. 1

(Pl. 24, Fig. 15, 17)

DESCRIPTION.—This taxon is similar to the nominate variety in all respects except size. These specimens are consistently 14–17 μm long and 5–7 μm wide, substantially smaller than the nominate variety according to Patrick and Reimer (1966: 452).
ECOLOGY.—Unknown.
DISTRIBUTION.—Frequent in sediments from Albany mudflat samples.

Navicula pygmeae Kutzing, 1849

(Pl. 24, Fig. 18; Pl. 25, Fig. 3, 4)

DESCRIPTION.—Patrick and Reimer 1966:442, pl. 39, fig. 4.
ECOLOGY.—Mesohalobous, benthic (Pankow 1976).
DISTRIBUTION.—Frequent in sediments from intertidal mud flats and salt marshes of present bay.

Navicula reichardtii var. *tschuktschorum* Cleve, 1895

(Pl. 25, Fig. 12)

DESCRIPTION.—Cleve (1895).
ECOLOGY.—Unknown, probably brackish water.
DISTRIBUTION.—Intertidal mud flats of present bay.

REMARKS.—Hustedt (1964:367) states that he doubts that this taxon belongs in *N. reichardtii.* Using the figures of Cleve (1895) he was unable to make a positive decision, but he indicated that the taxon may be a small species of *Diploneis.* For that reason Cleve's name is conserved in this study until further examination indicates otherwise. Van Landingham (1971) also places this taxon in *Diploneis.*

Navicula salinarum Grunow, 1880

(Pl. 24, Fig. 6–8)

DESCRIPTION.—Patrick and Reimer 1966:502, pl. 48, fig. 1. Hustedt 1930*b*:295, fig. 498.
ECOLOGY.—Brackish water, benthic, littoral (Patrick and Reimer 1966).
DISTRIBUTION.—Common in intertidal salt-marsh and mudflat sediments of present bay.

Navicula scopulorum Brébisson *in* Kutzing, 1849

(Pl. 25, Fig. 11)

DESCRIPTION.—Hendey 1964:193, pl. 30, fig. 6; pl. 41, fig. 1. Hustedt 1961:25, fig. 1186.
ECOLOGY.—Polyhalobous, meioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Rare, but widely distributed in Recent sediment from central and southern San Francisco Bay.

Navicula secreta var. *apiculata* Patrick, 1959

(Pl. 25, Fig. 10)

DESCRIPTION.—Patrick 1959:107, pl. 8, fig. 6.
ECOLOGY.—Fresh water, probably to slightly brackish, benthic.
DISTRIBUTION.—Two specimens from intertidal salt-marsh sediments.

Navicula spicula (Hickie) Cleve, 1894

(Pl. 25, Fig. 13)

DESCRIPTION.—Patrick and Reimer 1966:469, pl. 44, fig. 9.
ECOLOGY.—Marine to brackish water (Patrick and Reimer 1966).
DISTRIBUTION.—A single specimen from Recent sediment.

Navicula subforcipata Hustedt, 1964

(Pl. 25, Fig. 5)

DESCRIPTION.—Hustedt 1964:533, fig. 1569.
ECOLOGY.—Coastal marine, benthic (Hustedt 1966).
DISTRIBUTION.—Rare in Recent sediments from central San Francisco Bay.

Navicula tripunctata (O. F. Müler) Bory, 1824

(Pl. 25, Fig. 15–18)

DESCRIPTION.—Patrick and Reimer 1966:513, pl. 49, fig. 3, 4.
ECOLOGY.—Fresh to slightly brackish water (Patrick and Reimer 1966).

DISTRIBUTION.—Frequent in intertidal mud-flat sediments from the Albany mud flats and south of the Dumbarton Bridge; most abundant in a sample scraped off of a cobble from a stream bed in the mud flats. The sample was collected at low tide with fresh water flowing through the stream. At high tide the area is covered with brackish water reaching salinities 25‰.

Nitzschia Hassall, 1845

Nitzschia acuminata (Smith) Grunow, 1880

(Pl. 31, Fig. 7, 8)

DESCRIPTION.—Hendey 1964:280, pl. 39, fig. 10.

ECOLOGY.—Polyhalobous, meioeuryhaline, benthic (Pankow 1976); brackish water.

DISTRIBUTION.—Common and widespread in Sangamon and Recent sediments.

Nitzschia angularis Smith, 1853

(Pl. 33, Fig. 10)

DESCRIPTION.—Hendey 1964:281, pl. 39, fig. 6.

ECOLOGY.—Polyhalobous, meio- to mesoeuryhaline, benthic (Pankow 1976).

DISTRIBUTION.—Frequent in Recent sediment from intertidal mud-flat areas.

Nitzschia circumsuta (Bailey) Grunow, 1880

(Pl. 31, Fig. 9)

DESCRIPTION.—Hendey 1964:280, pl. 44, fig. 1.

ECOLOGY.—Mesohalobous, euryhaline, benthic (Pankow 1976).

DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Nitzschia closterium (Ehrenberg) Smith, 1853

(Pl. 33, Fig. 11)

DESCRIPTION.—Hendey 1964:283, pl. 21, fig. 8.

ECOLOGY.—Neritic plankton; marine to brackish water (Hendey 1964).

DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Nitzschia dissipata (Kutzing) Grunow, 1880

(Pl. 32, Fig. 11)

DESCRIPTION.—Hustedt 1930*b*:412, fig. 789.

ECOLOGY.—Oligohalobous "indifferent," mesoeuryhaline (Pankow 1976).

DISTRIBUTION.—A single specimen from Yerba Buena mud.

Nitzschia fasciculata Grunow *in* Van Heurck, 1880–1885

(Pl. 33, Fig. 14, 15)

DESCRIPTION.—Hustedt 1930*b*:421, fig. 815.

ECOLOGY.—Marine to brackish water, littoral, benthic (Hustedt 1930*b*).

DISTRIBUTION.—Frequent from intertidal mud-flat and salt-marsh samples, Recent sediments, Albany mud flats.

Nitzschia frustulum (Kutzing) Grunow, 1880

(Pl. 33, Fig. 1)

DESCRIPTION.—Lange-Bertalot and Simonsen 1978:23, fig. 1–39, 292, 293.

ECOLOGY.—An estuarine, brackish-water species.

DISTRIBUTION.—Rare, but widespread in Sangamon and Recent sediments.

Nitzschia gandersheimiensis Krasske, 1927

(Pl. 33, Fig. 2–4)

DESCRIPTION.—Lange-Bertalot and Simonsen 1978:28, fig. 40–53, 60–112, 289.

ECOLOGY.—Fresh to brackish water, seems to be typical of waters affected by industrial wastewater.

DISTRIBUTION.—Intertidal mud flats of present bay, common on Albany mud flats.

Nitzschia granulata Grunow, 1880

(Pl. 32, Fig. 2)

DESCRIPTION.—Hendey 1964:278. Schrader 1973, pl. 25, fig. 22.

ECOLOGY.—Marine to brackish, benthic, possibly epiphytic.

DISTRIBUTION.—Common and widely distributed in Sangamon and Recent sediments.

Nitzschia granulata var. 1

(Pl. 32, Fig. 3–5)

DESCRIPTION.—Valve elliptic to elliptic-lanceolate. Both margins furnished with short double rows of small punctae, one or two coarse punctae present at the end of each row. Axial area broad, lanceolate and hyaline, rarely interrupted by a few coarse punctae. Length, width, and striae as in nominate variety.

DISTRIBUTION.—Abundant in Sangamon and Recent sediments. Commonly in association with the nominate variety.

REMARKS.—This variety is distinguished from the nominate variety by the hyaline axial area. It is easily distinguished from *Nitzschia navicularis* by smaller size, coarser punctae, and the absence of an axial fold. In *Nitzschia navicularis,* both margins cannot be focused at the same time, whereas in this variety it is possible (see Pl. 32, Fig. 3–5 versus Fig. 1).

Nitzschia hummii Hustedt, 1955

(Pl. 33, Fig. 13)

DESCRIPTION.—Hustedt 1955:47, pl. 15, fig. 6.

ECOLOGY.—Brackish water, epipelagic (Hustedt 1955).

DISTRIBUTION.—A single specimen from the Yerba Buena mud.

REMARKS.—The reticulate pattern of striae on this species is very distinctive. However, this identification is quite doubtful because it is based on a single fragmentary specimen.

Nitzschia levidensis (Smith) Van Heurck, 1880–1885
(Pl. 31, Fig. 10)

DESCRIPTION.—Hendey 1964:277, pl. 44, fig. 4.
ECOLOGY.—Brackish water, benthic (Hendey 1964).
DISTRIBUTION.—Rare in Recent sediments.

Nitzschia longa Grunow, 1880
(Pl. 33, Fig. 9)

DESCRIPTION.—Hustedt 1955:46, pl. 16, fig. 1.
ECOLOGY.—Brackish water? (Hustedt 1955).
DISTRIBUTION.—A single specimen from Recent sediments.

Nitzschia navicularis (Brébisson) Grunow, 1880
(Pl. 32, Fig. 1)

DESCRIPTION.—Hendey 1964:276, pl. 39, fig. 3–5.
ECOLOGY.—A brackish-water species, benthic (Hendey 1964).
DISTRIBUTION.—Rare in Recent sediment.

Nitzschia obtusa var. *scalpeliformis* Grunow, 1878
(Pl. 33, Fig. 6)

DESCRIPTION.—Hustedt 1930*b*:422, fig. 817d.
ECOLOGY.—Marine to brackish water, littoral, benthic.
DISTRIBUTION.—Frequent in Recent sediment from intertidal mud flats, Albany mud flats.

Nitzschia panduriformis Gregory, 1857
(Pl. 32, Fig. 7)

DESCRIPTION.—Hendey 1964:279. Miller 1964:50, pl. 6, fig. 7.
ECOLOGY.—Polyhalobous, mesoeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Sangamon and Recent sediment, most abundant from intertidal mud flats of present bay.

Nitzschia plana Smith, 1853
(Pl. 32, Fig. 12)

DESCRIPTION.—Hendey 1964:278, pl. 39, fig. 7.
ECOLOGY.—Brackish water, benthic.
DISTRIBUTION.—Rare in Recent sediment.

Nitzschia pseudohybrida Hustedt, 1955
(Pl. 32, Fig. 9, 10)

DESCRIPTION.—Hustedt 1955:45, pl. 15, fig. 3, 4.
ECOLOGY.—Benthic, probably brackish water.
DISTRIBUTION.—Frequent in intertidal mud flats of present southern San Francisco Bay.

Nitzschia punctata (Smith) Grunow, 1880
(Pl. 31, Fig. 11–14)

DESCRIPTION.—Hendey 1964:278, pl. 39, fig. 11. Giffen 1970*a*:292, fig. 80. Cleve-Euler 1952:56, 57, fig. 1429.
ECOLOGY.—Polyhalobous, mesoeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Common and widespread in Sangamon and Recent sediment.

REMARKS.—This is one of the most common species of *Nitzschia* in the Sangamon and Recent flora. The specimens from San Francisco Bay show a wide range of sizes and shapes but seem clearly to belong to this species.

Nitzschia punctata var. *coarcta* (Grunow) Hustedt, 1921
(Pl. 32, Fig. 6)

DESCRIPTION.—Hendey 1964:278. Hasegawa 1975, pl. 10, fig. 8.
ECOLOGY.—Polyhalobous, meioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Sangamon and Recent sediment, rare.

Nitzschia pusilla (Kutzing) Grunow, 1880
(Pl. 32, Fig. 13–15)

DESCRIPTION.—Lange-Bertalot and Simonsen 1978, pl. 11, fig. 198–202. Lange-Bertalot 1977:273, pl. 7, fig. 1–10.
DISTRIBUTION.—Intertidal mud flats and salt marshes of present bay.

Nitzschia sigma (Kutzing) Smith, 1853
(Pl. 33, Fig. 16–18)

DESCRIPTION.—Hendey 1964:281, pl. 42, fig. 1. Hustedt 1930*b*:420, fig. 813.
ECOLOGY.—Marine to brackish, mesohalobous, holoeuryhaline (Pankow 1976), benthic.
DISTRIBUTION.—Widespread but not common in Recent and Sangamon sediments.

Nitzschia sigmaformis Hustedt, 1955
(Pl. 33, Fig. 7, 8)

DESCRIPTION.—Hustedt 1955:47, pl. 16, fig. 2, 3.
ECOLOGY.—Brackish water, estuarine, benthic.
DISTRIBUTION.—Frequent in Recent sediment from intertidal mud flats, Albany mud flats.

Nitzschia tryblionella Hantzsch *in* Rabenhorst, 1848–1860
(Pl. 31, Fig. 4–6)

DESCRIPTION.—Hendey 1964:276, pl. 44, fig. 2, 3.
ECOLOGY.—Oligohalobous (halophile), pleio- to mesoeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Widespread in Sangamon and Recent sediment, most abundant in sediments from intertidal mud flats of present bay.

Nitzschia tryblionella var. *victorae* Grunow, 1863
(No illustration)

DESCRIPTION.—Hustedt 1930*b*:399, fig. 758.
ECOLOGY.—Same as species.
DISTRIBUTION.—Rare in Recent sediments.

Nitzschia vitrea Norman, 1861
(Pl. 33, Fig. 5)

DESCRIPTION.—Hustedt 1930*b*:411, fig. 787.
ECOLOGY.—Mesohalobous, euryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

REMARKS.—These specimens are questionably assigned to *N. vitrea*. The keel puncta and striae are finer (10–14 in 10 μm and 30–35 in 10 μm, respectively) than that which Hustedt (1930*b*) gives for *N. vitrea* (4–7 in 10 μm and 17–27 in 10 μm, respectively). However, such variation in a single species is quite common (see Lange-Bertalot 1977; Lange-Bertalot and Simonsen 1978).

Nitzschia sp. 1
(Pl. 32, Fig. 8)

DESCRIPTION.—Valves elliptic-lanceolate with slightly cuneate apices, 14–16 μm long, 6 μm wide. Valve with transverse costae (16–18 in 10 μm). A longitudinal line runs parallel to the margin, close to the side opposite the keel. A few scattered punctae occur along this margin.
DISTRIBUTION.—Frequent in Recent sediments from Suisun Bay.

Opephora Petit, 1888

Opephora swartzii (Grunow) Petit *in* Pelletan, 1889
(Pl. 16, Fig. 1, 2)

DESCRIPTION.—Patrick and Reimer 1966:116, pl. 3, fig. 1.
ECOLOGY.—Brackish to marine waters, benthic.
DISTRIBUTION.—Rare in Sangamon sediments.

Opephora pacifica (Grunow) Petit, 1888
(Pl. 16, Fig. 3)

DESCRIPTION.—Hustedt 1931:135, fig. 655. Hustedt 1955: 13, pl. 4, fig. 47–49.
ECOLOGY.—Marine, littoral species, benthic (Hustedt 1931).
DISTRIBUTION.—Rare in Recent sediments.

Paralia Heiberg, 1863

Paralia sulcata (Ehrenberg) Cleve, 1873
(Pl. 2, Fig. 5–17)

DESCRIPTION.—Crawford 1979:200–210, fig. 1–33.
ECOLOGY.—Polyhalobous, mesoeuryhaline (Pankow 1976).
DISTRIBUTION.—Abundant and widespread in Sangamon and Recent sediment.

REMARKS.—Two varieties, the nominate and *P. sulcata* var. *coronata* (Ehr.) Andrews, are recognized by many authors. Crawford (1979) has shown that *P. sulcata* (Ehr.) Cleve is heterovalvar with valves assignable to both varieties present in a single cell. Both varieties occur in the material from San Francisco Bay, but I did not treat them separately. Plate 2, Figures 6 and 11 show opposite valves of a single cell illustrating both varieties and thus supporting Crawford's (1979) findings.

Pinnularia Ehrenberg, 1843

Pinnularia abaujensis var. *rostrata* (Patrick) Patrick *in* Patrick and Reimer, 1966
(Pl. 26, Fig. 7)

DESCRIPTION.—Patrick and Reimer 1966:614, pl. 58, fig. 4.
ECOLOGY.—Fresh water (Patrick and Reimer 1966).
DISTRIBUTION.—A single specimen in Sangamon sediments.

Pinnularia acuminata Smith, 1853
(Pl. 26, Fig. 6)

DESCRIPTION.—Patrick and Reimer 1966:621, pl. 59, fig. 4.
ECOLOGY.—Fresh water (Patrick and Reimer 1966).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Pinnularia borealis Ehrenberg, 1843
(Pl. 25, Fig. 14)

DESCRIPTION.—Patrick and Reimer 1966:618, pl. 58, fig. 13.
ECOLOGY.—Fresh water, low mineral-content.
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Pinnularia borealis var. *brevicostata* Hustedt, 1914
(Pl. 26, Fig. 2)

DESCRIPTION.—Hustedt1930*b*:326, fig. 598.
ECOLOGY.—Same as species.
DISTRIBUTION.—A single specimen in the Yerba Buena mud.

Pinnularia gibba Ehrenberg, 1841
(Pl. 26, Fig. 4, 5)

DESCRIPTION.—Hustedt 1930*b*:327, fig. 600b.
ECOLOGY.—Fresh water (Hustedt 1930*b*).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Pinnularia microstauron var. *biundulata* O. Muller, 1893
(Pl. 26, Fig. 8)

DESCRIPTION.—Hustedt 1930*b*:320, fig. 583.
ECOLOGY.—Fresh water (Hustedt 1930*b*).
DISTRIBUTION.—A single specimen from the Yerba Buena mud.

Pinnularia subcapitata var. *paucistriata* (Grunow) Cleve, 1895
(Pl. 26, Fig. 3)

DESCRIPTION.—Patrick and Reimer 1966:597, pl. 55, fig. 11.
ECOLOGY.—Fresh water, low mineral-content.
DISTRIBUTION.—A single specimen from Recent sediment.

Plagiogramma Greville, 1859

Plagiogramma interruptum (Greville) Ralfs, 1861

(No illustration)

DESCRIPTION.—Hustedt 1931:110, fig. 656.
ECOLOGY.—Marine to brackish, warm water (Hustedt 1931).
DISTRIBUTION.—Rare in Sangamon sediments.

Plagiogramma staurophorum (Gregory) Heiberg, 1863

(No illustration)

DESCRIPTION.—Hendey 1964:166, pl. 36, fig. 1.
ECOLOGY.—Polyhalobous, meioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—A single specimen in the Yerba Buena mud.

Plagiotropis Pfitzer, 1871

Plagiotropis vitrea (Smith) comb. nov.

(Pl. 27, Fig. 2, 3)

DESCRIPTION.—Hendey 1964:255, pl. 36, fig. 3 (as *Tropidoneis vitrea*).
ECOLOGY.—Benthic, marine and brackish water (Hendey 1964).
DISTRIBUTION.—Common in sediments from intertidal mud flats and salt marshes, present bay.

REMARKS.—Patrick and Reimer (1975) point out that Cleve (1891) placed all of *Plagiotropis* Pfitzer (1871), including the type species, in his new genus *Tropidoneis*. Therefore, according to priority and Article 57.1 of the *International Code of Botanical Nomenclature (1978), Plagiotropis* is the legal name for this genus. Simonsen (1979: 53) also recognizes *Plagiotropis* as the valid generic designation.

Pleurosigma Smith, 1852

Pleurosigma angulatum (Quekett) Smith, 1852

(Pl. 20, Fig. 7; Pl. 21, Fig. 8)

DESCRIPTION.—Patrick and Reimer 1966:331, pl. 27, fig. 1a–c.
ECOLOGY.—Polyhalobous, mesoeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Rare in intertidal mud-flat sediments, present bay.

Pleurosigma australe Grunow, 1868*b*

(Pl. 21, Fig. 6, 7)

DESCRIPTION.—Patrick and Reimer 1966:336, pl. 28, fig. 3a–c.
ECOLOGY.—Insufficiently known.
DISTRIBUTION.—Rare in intertidal mud-flat sediments of present bay.

Pleurosigma diverse-striatum Meister, 1935

(Pl. 20, Fig. 6)

DESCRIPTION.—Hendey 1958:58, 1970:152, pl. 6, fig. 62.
ECOLOGY.—Marine to brackish water, littoral, benthic.
DISTRIBUTION.—Frequent and widespread in the Yerba Buena mud, rare in Recent sediment.

Pleurosigma formosum Smith, 1852

(Pl. 21, Fig. 5)

DESCRIPTION.—Hendey 1951:62, pl. 11, fig. 6.
ECOLOGY.—A marine species, favors high salinity (Hendey 1964).
DISTRIBUTION.—A single specimen from Recent sediment.

Pleurosigma normanii Ralfs *in* Pritchard, 1861

(Pl. 20, Fig. 11, 12)

DESCRIPTION.—Hendey 1964:244. Cleve-Euler 1952:22, fig. 1371, pl. F, fig. f.
ECOLOGY.—Polyhalobous, meioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Common in the Yerba Buena mud, present in Recent sediments.

REMARKS.—Transverse striae on specimens from the Yerba Buena mud range from 21–25 in 10 μm, somewhat finer than is typical (19–21 in 10 μm).

Pleurosigma strigosum Smith, 1852

(Pl. 21, Fig. 1–4)

DESCRIPTION.—Patrick and Reimer 1966:335, pl. 28, fig. 2a–c. Cleve-Euler 1952:22, fig. 1369.
ECOLOGY.—Polyhalobous, meioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Common in intertidal mud-flat and salt-marsh samples of present bay.

Pleurosigma sp. 1

(Pl. 20, Fig. 8, 9)

DESCRIPTION.—Valves linear to linear-lanceolate, sigmoid with subacute apexes. Margins parallel in middle half of valve. Raphe strongly sigmoid and eccentric towards the ends. Polar and central nodules small. Central nodule ovoid. Axial area narrow to absent. Valve striate, striae cross at 70–75° angle, transverse striae 16–18 in 10 μm. Length 220–250 μm, breadth 26–27 μm.
DISTRIBUTION.—Recent intertidal mud-flat sediments.

REMARKS.—This species superficially resembles *P. formosum* Smith and may represent small specimens of that species. *Pleurosigma formosum* is typically longer than 300 μm (Hendey 1951, 1964), whereas these specimens are less than 300 μm long. In addition, the striae are somewhat finer (16–18 in 10 μm) on this species than on *P. formosum* (14–16 in 10 μm), and the

angle between oblique striae is 70–75° versus 90° in *P. formosum.*

Pleurosigma sp. 2
(Pl. 20, Fig. 10)

DESCRIPTION.—Valve slightly sigmoid, linear-lanceolate with subacute apexes. Valve surface slightly arched at ends. Raphe sigmoid, slightly eccentric at ends. Axial area narrow. Central nodule small, ovate. Transverse striae 20–24 in 10 μm. Length 160–175 μm, breadth 30–32 μm.
DISTRIBUTION.—Rare in sediments from intertidal mud flats of present bay, Albany mud flats.

REMARKS.—This species most closely resembles *P. strigosum* Smith, but is more finely striate than that species. Otherwise, it is quite similar to smaller specimens of *P. strigosum.*

Pseudoeunotia Grunow, 1880

Pseudoeunotia doliolus (Wallich) Grunow *in* Van Heurck, 1880
(Pl. 31, Fig. 1)

DESCRIPTION.—Schrader 1973:708, pl. 4, fig. 1–8. Hustedt 1959:258–260.
ECOLOGY.—Marine, oceanic, planktonic.
DISTRIBUTION.—Rare in Recent sediments.

Rhabdonema Kutzing, 1844

Rhabdonema arcuatum (Agardh) Kutzing, 1844
(Pl. 16, Fig. 5)

DESCRIPTION.—Hustedt 1931:20, fig. 549.
ECOLOGY.—Polyhalobous, meioeuryhaline, epiphytic (Pankow 1976).
DISTRIBUTION.—Rare in Sangamon sediments.

Rhaphoneis Ehrenberg, 1844

Rhaphoneis amphiceros (Ehrenberg) Ehrenberg, 1844
(Pl. 16, Fig. 6)

DESCRIPTION.—Hendey 1964:154, pl. 26, fig. 1–4.
ECOLOGY.—Marine neritic, benthic (Hendey 1964).
DISTRIBUTION.—Frequent and widespread in the Yerba Buena mud but rare in Recent sediments.

Rhaphoneis margaritalimbata Mertz, 1966
(Pl. 16, Fig. 7)

DESCRIPTION.—Mertz 1966:27, pl. 6, fig. 1–3.
ECOLOGY.—Marine (Mertz 1966; Schrader 1973).
DISTRIBUTION.—Rare, but widespread in Sangamon and Recent sediment.

Rhaphoneis surirella (Ehrenberg) Grunow *in* Van Heurck, 1880
(Pl. 16, Fig. 8)

DESCRIPTION.—Hendey 1964:155, pl. 26, fig. 11–13.
ECOLOGY.—Polyhalobous, meioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—Rare in Recent and Sangamon sediments.

Rhizosolenia Brightwell, 1858

Rhizosolenia sp. 1
(Pl. 14, Fig. 9)

This species is rare in Sangamon and Recent sediment and is represented only by isolated apical spines. No effort was made to determine the species.

Rhoicosphenia Grunow, 1860

Rhoicosphenia curvata (Kutzing) Grunow *in* Rabenhorst, 1864
(Pl. 19, Fig. 6)

DESCRIPTION.—Patrick and Reimer 1966:282, pl. 20, fig. 1–5.
ECOLOGY.—Oligohalobous, halo- to pleioeuryhaline, benthic (Pankow 1976); fresh to brackish water.
DISTRIBUTION.—Rare but widespread in Sangamon sediments, common in intertidal mud-flat and salt-marsh sediments of present bay.

Rhopalodia O. Muller, 1895

Rhopalodia gibba (Ehrenberg) O. Muller, 1895
(Pl. 30, Fig. 6)

DESCRIPTION.—Patrick and Reimer 1975:189, pl. 28, fig. 1.
ECOLOGY.—Oligohalobous "indifferent," mesohalobous, benthic (Pankow 1976); epiphytic.
DISTRIBUTION.—Rare, but widespread in Sangamon and Recent sediment.

Rhopalodia gibberula (Ehrenberg) O. Muller, 1895
(Pl. 30, Fig. 7–10)

DESCRIPTION.—Patrick and Reimer 1975:191, pl. 28, fig. 6.
ECOLOGY.—Oligohalobous ("indifferent" to halophilic), pleioeuryhaline (Pankow 1976).
DISTRIBUTION.—Rare in Recent sediment and Sangamon sediment.

Rhopalodia operculata (Agardh) Hakansson, 1979
(Pl. 30, Fig. 11)

DESCRIPTION.—Hakansson 1979:1, 66, fig. 1–5.
DISTRIBUTION.—Present in Sangamon and Recent sediments.

REMARKS.—Hakansson (1979) synonymized *R. musculus* (Kutzing) O. Muller with *R. operculata* on the basis of priority after examination of Agardh's type material of "Frustulia operculata" and "Cymbella operculata." Patrick and Reimer (1975:191–192) indicate that *R. gibberula* (Ehrenberg) O. Muller and *R. musculus* (Kutz.) Muller are very similar, closely related, and possibly synonymous. These species are distinguished by shape alone, being identical in all other characters. Pankow (1976) recognizes *R. musculus* as a variety of *R. gibberula.* Apparently, recognition of these species is more than ordinarily subjective and will undoubtedly be subject to equivocation. Therefore, only *R. operculata* is recognized in this study.

Scoliopleura Grunow, 1860

Scoliopleura tumida (Brébisson *in* Kutzing) Rabenhorst, 1864

(Pl. 26, Fig. 9)

DESCRIPTION.—Hendey 1964:234, pl. 29, fig. 6, 7.
ECOLOGY.—Brackish-water, euryhaline.
DISTRIBUTION.—Rare in Recent sediments.

Scoliotropis Cleve, 1894

Scoliotropis latestriata (Brébisson *in* Kutzing) Cleve, 1894

(Pl. 26, Fig. 12)

DESCRIPTION.—Hendey 1951:64, pl. 11, fig. 3, 4.
ECOLOGY.—Polyhalobous, meioeuryhaline, benthic (Pankow 1976).
DISTRIBUTION.—A single specimen from the Yerba Buena mud.

Skeletonema Greville, 1865

Skeletonema costatum (Greville) Cleve, 1878

(No illustration)

DESCRIPTION.—Hendey 1964:91, pl. 7, fig. 3.
ECOLOGY.—Polyhalobous, pleioeuryhaline (Pankow 1976); arctic, neritic plankton (Hendey 1964).
DISTRIBUTION.—Rare in Recent sediments.

REMARKS.—Although this species is abundant at times in the plankton of San Francisco Bay (Wong and Cloern 1981), it is extremely rare in the sediments. This is probably because its delicate frustule is destroyed by dissolution and bioturbation.

Stauroneis Ehrenberg, 1843

Stauroneis acuta Smith, 1853

(Pl. 22, Fig. 1)

DESCRIPTION.—Patrick and Reimer 1966, pl. 31, fig. 1.
ECOLOGY.—Alkaliphilous, oligohalobous (Patrick and Reimer 1966).
DISTRIBUTION.—Rare in Sangamon and Recent sediment.

Stauroneis amphioxys Gregory, 1856

(Pl. 22, Fig. 2)

DESCRIPTION.—Patrick and Reimer 1966, pl. 30, fig. 7. Hendey 1964:219, pl. 37, fig. 13, 14.
ECOLOGY.—Mesohalobous, euryhaline, benthic (Pankow 1976); euryhaline, brackish to marine (Patrick and Reimer 1966).
DISTRIBUTION.—Common in sediments from intertidal salt marsh and mud flats of present bay, Albany mud flats.

Stauroneis obtusa Lagerstedt, 1873

(Pl. 21, Fig. 9)

DESCRIPTION.—Patrick and Reimer 1966:363, pl. 30, fig. 8, 9.
ECOLOGY.—Oligohalobous ("indifferent" to halophobic), alkaliphilous.
DISTRIBUTION.—A single specimen from the Yerba Buena mud.

REMARKS.—Pseudosepta are not conspicuous on this specimen and may have been removed by breakage or dissolution. The specimen agrees in all other respects with the diagnosis of *S. obtusa.*

Stauroneis smithii var. *incisa* Pantocsek, 1902

(Pl. 21, Fig. 10)

DESCRIPTION.—Patrick and Reimer 1966:366, pl. 30, fig. 13.
ECOLOGY.—Fresh water (Patrick and Reimer 1966).
DISTRIBUTION.—A single specimen from the Yerba Buena mud.

Stephanodiscus Ehrenberg, 1845

Stephanodiscus astrea (Ehrenberg) Grunow, 1880

(Pl. 4, Fig. 9, 10)

DESCRIPTION.—Hustedt 1930*b*:368, fig. 193. Schrader 1978: 863, pl. 2, fig. 7, 11; pl. 3, fig. 11, 12; pl. 4, fig. 22, 23; pl. 13, fig. 2, 8.
ECOLOGY.—Planktonic; oligohalobous, meioeuryhaline (Pankow 1976); marine to brackish water (Hendey 1964:75 as *S. rotula*).
DISTRIBUTION.—Common in Recent sediments from intertidal mud flats of Northern San Francisco, San Pablo, and Suisun bays.

REMARKS.—Hendey (1964) synonymized *S. astrea* with *S. rotula* Kutzing. Pankow (1976)

recognized this synonymy whereas Schrader (1978) did not. According to Hustedt (1928, 1930*a*), Cholnoky (1968), Pankow (1976), and Schrader (1978), *S. astrea* is a freshwater species common in lakes and streams, but it can tolerate slightly brackish water. Hendey (1964:75) states that *S. rotula* is a "marine to brackish-water species widespread and common on all european coasts, particularly in estuaries and waters of lowered salinity."

Stephanodiscus carconensis Eulenstein *in* Grunow, 1878

(Pl. 4, Fig. 1–4)

DESCRIPTION.—Van Landingham 1967:17, pl. 21, fig. 18. Schrader 1978:863, pl. 9, fig. 5, 8, 11–15, 18–23, 27.
ECOLOGY.—Planktonic, fresh water (Schrader 1978).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Stephanodiscus lucens Hustedt, 1939

(No illustration)

DESCRIPTION.—Hustedt 1939:583, 584, fig. 4
ECOLOGY.—Probably fresh water.
DISTRIBUTION.—Rare in Recent sediments from Suisun Bay.

Stephanodiscus niagarae Ehrenberg, 1841

(Pl. 4, Fig. 5–8)

DESCRIPTION.—Schrader 1978:863, pl. 5, fig. 1; pl. 6, fig. 5; pl. 7, fig. 10; pl. 8, fig. 1; pl. 16, fig. 1; pl. 17, fig. 1, 2.
ECOLOGY.—Planktonic, fresh water, oligotrophic, moderate temperatures, pH-neutral (Schrader 1978).
DISTRIBUTION.—Widespread but not abundant in Sangamon and Recent sediments.

Stephanogonia Ehrenberg, 1844

Stephanogonia? sp. 1

(No illustration)

This taxon is represented by a single fragmentary specimen from Recent sediments. No diagnosis is attempted based on this specimen, which is questionably assigned to *Stephanogonia.*

Stephanopyxis Ehrenberg, 1844

Stephanopyxis turris (Greville and Arv.) Ralfs *in* Pritchard, 1861

(No illustration)

DESCRIPTION.—Hendey 1964:92. Schrader 1973, pl. 15, fig. 1–7.
ECOLOGY.—Polyhalobous, pleioeuryhaline, planktonic (Pankow 1976).
DISTRIBUTION.—Rare in Sangamon sediments.

Stephanopyxis? sp. 1

(Pl. 6, Fig. 5)

DESCRIPTION.—Valve circular, flat, with coarse areolae in linear array, areolae 8 in 10 μm and uniform in size across valve face. Mantle deep with coarse areolae, 8 in 10 μm, only slightly smaller than on valve face. Diameter 26 μm.
DISTRIBUTION.—One specimen from Recent sediments.

REMARKS.—This specimen is similar in size and shape to the lower valves of several dimorphic species of *Stephanopyxis* described by Schrader (1973). However, in contrast to the specimen figured here, the areolae on those species are not uniform in size across the valve face and are arranged in tangential rows.

Surirella Turpin, 1828

Surirella crumena Brébisson *in* Kutzing, 1849

(Pl. 34, Fig. 6, 7)

DESCRIPTION.—Schmidt 1878–1959, pl. 24, fig. 7–9. Hendey 1964:288, pl. 40, fig. 12. Pankow 1976:316, pl. 21, fig. 4, as *S. ovalis* var. *crumena.*
ECOLOGY.—Oligohalobous (halophilic) (Pankow 1976).
DISTRIBUTION.—Rare in Sangamon sediment.

Surirella fastuosa (Ehrenberg) Kutzing, 1844

(Pl. 34, Fig. 3, 5)

DESCRIPTION.—Hendey 1964:288, pl. 40, fig. 4.
ECOLOGY.—Marine to brackish water, benthic.
DISTRIBUTION.—Recent surface sediment.

Surirella gemma (Ehrenberg) Kutzing, 1844

(Pl. 34, Fig. 8)

DESCRIPTION.—Hendey 1964:288, pl. 40, fig. 5.
ECOLOGY.—Mesohalobous, benthic (Pankow 1976).
DISTRIBUTION.—Rare in Sangamon sediment; frequent and widespread in Recent sediment; most common from intertidal mud flats.

Surirella ovata Kutzing, 1844

(Pl. 34, Fig. 2)

DESCRIPTION.—Hendey 1951:77, pl. 14, fig. 4–7.
ECOLOGY.—Oligohalobous "indifferent", mesoeuryhaline (Pankow 1976); common in brackish waters (Hendey 1964).
DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Surirella peisonis Pantocsek, 1889

(Pl. 34, Fig. 9)

DESCRIPTION.—Hustedt 1930*b*:441, fig. 862.
ECOLOGY.—Brackish to marine water, benthic (Hustedt 1930*b*).
DISTRIBUTION.—A single specimen from Recent sediment in Suisun Bay.

REMARKS.—Cleve-Euler (1952) and Pankow

(1976) have synonymized *S. peisonis* with *S. ovalis* var. *pyriformis* (Pantocsek) Cleve-Euler. Hustedt (1930*b*) indicated that *S. pyriformis* Pantocsek is synonymous with *S. peisonis*. Van Landingham (1978, VII) synonymizes *peisonis* with *S. ovalis* var. *maxima* Grunow.

Surirella recedens Schmidt, 1874

(No illustration)

DESCRIPTION.—Hendey 1970:159, pl. 5, fig. 45. Hustedt 1955: 48, pl. 3, fig. 2.

ECOLOGY.—Marine to brackish water (Hendey 1970).

DISTRIBUTION.—Rare, but widespread in Recent and Sangamon sediments.

Surirella salina Smith, 1851

(No illustration)

DESCRIPTION.—Hendey 1964:287, pl. 40, fig. 11.

ECOLOGY.—A brackish-water species.

DISTRIBUTION.—A single specimen from the Yerba Buena mud.

REMARKS.—This specimen is fragmental and is questionably assigned to *S. salina*. Cleve-Euler (1952) considered this taxon to be a variety of *S. ovalis* Breb.

Surirella striatula Turpin, 1828

(Pl. 34, Fig. 1)

DESCRIPTION.—Hendey 1964:288, pl. 40, fig. 2, 3.

ECOLOGY.—Mesohalobous (Pankow 1976); brackish water, benthic.

DISTRIBUTION.—Widespread in Recent and Sangamon sediment.

Surirella torquata Pantocsek, 1892

(Pl. 34, Fig. 4)

DESCRIPTION.—Pantocsek 1892, pl. 41, fig. 570; 1905:102. Cleve-Euler 1952:124, fig. 1568b.

ECOLOGY.—Benthic, brackish water (Cleve-Euler 1952).

DISTRIBUTION.—Widespread and frequent in Recent sediment.

REMARKS.—This taxon is questionably assigned to *S. torquata* because a complete description is not available. Cleve-Euler's (1952) illustration shows a striate valve, whereas these valves appear punctate.

Tabellaria Ehrenberg, 1840

Tabellaria fenestra (Lyngbye) Kutzing, 1844

(Pl. 16, Fig. 10)

DESCRIPTION.—Patrick and Reimer 1966:103, pl. 1, fig. 1, 2.

ECOLOGY.—Oligohalobous, meioeuryhaline, benthic (Pankow 1976).

DISTRIBUTION.—Rare in Recent sediments.

Terpsinoe Ehrenberg, 1843

Terpsinoe americana (Bailey) Ralfs *in* Pritchard, 1861

(Pl. 14, Fig. 6, 7)

DESCRIPTION.—Hustedt 1930*a*:900, fig. 541.

ECOLOGY.—Marine to brackish water; littoral in the subtropical coast of South Africa (Cholnoky 1968), benthic.

DISTRIBUTION.—Frequent in a single sample from the Yerba Buena mud, rare elsewhere in Sangamon sediment.

REMARKS.—This appears to be the first record of this species from the west coast of North America.

Thalassionema (Grunow) Hustedt, 1932

Thalassionema nitzschioides Hustedt, 1932

(Pl. 16, Fig. 9)

DESCRIPTION.—Hendey 1964:165. Hasle and de Mendiola 1967:111, fig. 5, 27–34, 39–44.

ECOLOGY.—Polyhalobous, meio- to mesoeuryhaline (Pankow 1976); neritic plankton common in upwelling areas.

DISTRIBUTION.—Abundant and widespread in the Yerba Buena mud, widespread but rare in Recent sediments.

Thalassiosira Cleve, 1873

Thalassiosira decipiens (Grunow) Jorgensen, 1905

(Pl. 12, Fig. 1–4)

DESCRIPTION.—Hasle 1979:85–108, fig. 1–42.

ECOLOGY.—Marine to brackish water, littoral, probably benthic, epiphytic, living in chains attached at one end to a substrate; reported from rivers, estuaries and inland salt waters (Hasle 1979).

DISTRIBUTION.—Abundant and widespread in Recent sediments especially in Suisun Bay where it was the dominant diatom. Widespread but not abundant in Sangamon sediments.

REMARKS.—This species is quite variable with respect to convexity of the valve and the pattern and density of areolae. The areolae vary from polygonal (usually hexagonal) to circular. These features are shown also by the figures of Hasle (1979). On the basis of these characters two forms could be recognized. One morph has a slightly convex to nearly flat valve and densely spaced, polygonal areolae (Pl. 12, fig. 1–4). This form is referred to as *T. decipiens*. The other form, referred to as *T. decipiens* var. 1, has a strongly convex valve, with widely spaced, round areolae arranged in a radial pattern. Compare figures 21–

23 with figure 25 of Hasle (1979). Nevertheless, the pattern of strutted and labiate processes in that form is consistent with the nominate variety. However, features such as the number and position of strutted and labiate processes are difficult to assess for each specimen in whole-sample strewn amounts of acid-cleaned sediment. For this reason it is difficult to accurately and consistently distinguish between *T. decipiens* and closely related species such as *T. incerta, T. angulata,* and *T. visurgis* when examining tens of thousands of specimens. Although no specimens assignable to those species were observed, it is probably best to consider this taxon as a species group.

Thalassiosira decipiens var. 1
(Pl. 12, Fig. 5–9)

DESCRIPTION.—This variety is identical to the nominate variety regarding number and distribution of labiate and strutted processes. It is typically smaller (9–16 μm diameter) compared to the nominate variety, which reaches a maximum diameter of about 25 μm in these samples. Variety 1 has a strongly convex valve. The areolae are round and widely spaced in radiate rows. In some specimens the central area is hyaline except for a single strutted process.

DISTRIBUTION.—Widespread in Recent sediment especially in Suisun and San Pablo Bays.

REMARKS.—Although Hasle (1979) includes forms similar to this variety in the nominate variety (see fig. 25, Hasle 1979), this variety is easily recognizable and shows a distinct distributional pattern in Recent sediments of the bay (Laws 1983*b*). Therefore, it is recorded in this study as a distinct variety. Future studies may show that the morphological and geographical separation of these varieties is not real.

Thalassiosira eccentrica (Ehrenberg) Cleve, 1904
(Pl. 10, fig. 6, 7; Pl. 11, fig. 1–9)

DESCRIPTION.—Fryxell and Hasle 1972:300–312, fig. 1–18.

ECOLOGY.—Planktonic, typically marine neritic but present in oceanic plankton.

DISTRIBUTION.—Rare, but widespread in Sangamon and Recent sediment.

REMARKS.—According to Fryxell and Hasle (1972:302), the pattern of areolae is that of "... eccentric (rather than concentric) arcs, grading into fasciculated structure on some valves." Furthermore, Fryxell and Hasle indicate that the number and distribution of tubular processes are more valuable diagnostic characters. Therefore, I have adopted a broad concept of areolation in *T. eccentrica,* while adhering strictly to their description of position and number of tubular processes (i.e., one central strutted tubulus, one large marginal labiate process, a double row of marginal strutted tubuli, and strutted tubuli scattered evenly over the valve face).

Thalassiosira hendeyi Hasle and Fryxell, 1977
(Pl. 10, Fig. 2–5)

DESCRIPTION.—Hasle and Fryxell 1977:25, fig. 35–45.

ECOLOGY.—Planktonic, coastal marine, warm water.

DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Thalassiosira lacustris (Grunow) Hasle, 1977
(Pl. 6, fig. 7, 8; Pl. 7, Fig. 1, 2)

DESCRIPTION.—Hustedt 1928:432, fig. 235 (as Coscinodiscus lacustris); Hasle and Fryxell 1977:40.

ECOLOGY.—Probably mesohalobous, coastal marine, planktonic, and benthic (Pankow 1976).

DISTRIBUTION.—Widespread in Sangamon and Recent sediment, most abundant in samples from Suisun and San Pablo bays.

REMARKS.—Two morphs are present in this material. One is robust and corresponds to var. *hyperborea* Grunow (Hustedt 1928:433, fig. 235c); the other probably corresponds to the more delicate variety *septentrionalis* Grunow (Hustedt 1928, Fig. 235d). The robust forms show 10–14 large marginal spines and a double row of tubular processes along the margin (Pl. 7, Fig. 1). The lightly silicified delicate forms have a single ring of small marginal processes (7 in 10 μm, see Pl. 7, Fig. 2), which appear to penetrate the valve surface and are suggestive of strutted processes.

Thalassiosira nodulolineata (Hendey) Hasle and Fryxell, 1977
(Pl. 10, Fig. 1)

DESCRIPTION.—Hasle and Fryxell 1977:35, fig. 86–93.

ECOLOGY.—Planktonic, coastal marine and brackish water.

DISTRIBUTION.—Rare in Sangamon sediments; frequent and widespread in Recent sediments, most common in Suisun and San Pablo bays.

Thalassiosira cf. *T. pacifica* Gran and Angst, 1931
(Pl. 11, Fig. 9)

DESCRIPTION.—Gran and Angst 1931:437, fig. 12.

ECOLOGY.—Poorly known.

DISTRIBUTION.—Very rare in Sangamon sediments.

REMARKS.—Identification of this species is dif-

ficult because the original description and figures have not been emended to include characters presently used to distinguish species of *Thalassiosira*. The specimen pictured in Plate 11, Figure 9 shows the fasciculated pattern described by Gran and Angst (1931). It also shows a single row of marginal tubuli, which may correspond to the single row of marginal "spinules" described by Gran and Angst; but this specimen is larger than theirs (72 μm versus 46 μm). Schrader (1973) and Barron (1975) figure specimens of *T. pacifica*. Schrader's specimens are the proper size but show eccentric rather than fasciculated areolae. Schrader states that his identifications were based on comparison with specimens figured by Jousé (1962). Specimens figured by Barron (1975, pl. 14, fig. 7, 8) compare more favorably to the original description, but one specimen is much larger (100 μm), and neither illustration shows marginal tubuli.

Thalassiosira punctigera (Castracane) Hasle, 1983
(Pl. 9, Fig. 7, 8)

DESCRIPTION.—Gran and Angst 1931:443, fig. 19, 20 as *Coscinodiscus angstii*. Hasle (1983).

ECOLOGY.—Planktonic, marine to brackish water, originally described from Puget Sound.

DISTRIBUTION.—Rare in Recent sediment of Central San Francisco Bay and San Pablo Bay.

REMARKS.—These specimens are questionably assigned to *T. punctigera*. The circlet of large, marginal processes shown by Gran and Angst (1931) and Fryxell (1975, fig. 25, 26) are not evident on these specimens. Other features agree with the diagnosis of *T. punctigera*. The diameter of these specimens reaches 115 μm.

Thalassiosira sp. 1
(Pl. 9, Fig. 6)

DESCRIPTION.—Valve circular, flat. Mantle distinct in valve view, about one-sixth the diameter; diameter 26 μm. Areolae small, circular, in radial rows arranged in indistinct bundles with on overprinted concentric pattern (a Fibbonaci sequence). Areolae in central area larger (15–18 in 10 μm) than near the margin where they are 25–30 in 10 μm. A single central pore (strutted process) adjacent to central areolae. Pores scattered on valve face. A single row of marginal pores, seven to nine in 10 μm. Seven to eight large tubuli (labiate processes) around the margin at irregular intervals. A single row of spines around the margin, 13–14 in 10 μm.

DISTRIBUTION.—A single specimen from the Yerba Buena mud.

Trachyneis Cleve, 1894

Trachyneis aspera (Ehrenberg) Cleve, 1894
(Pl. 29, Fig. 13)

DESCRIPTION.—Hendey 1964:236, pl. 29, fig. 13.

ECOLOGY.—Polyhalobous, meioeuryhaline, benthic (Pankow 1976).

DISTRIBUTION.—Rare in Sangamon and Recent sediments.

Trachysphenia Petit, 1877

Trachysphenia acuminata Peragallo *in* Temperé and Peragallo, 1910
(Pl. 16, Fig. 11)

DESCRIPTION.—Hustedt 1955:14, pl. 4, fig. 50–54.

ECOLOGY.—Benthic, brackish water, epiphytic.

DISTRIBUTION.—Widespread but not common in Sangamon and Recent sediments.

Triceratium Ehrenberg, 1841

Triceratium dubium Brightwell, 1859
(Pl. 14, Fig. 8)

DESCRIPTION.—Hustedt 1930*a*:806, fig. 469. Hendey 1970: 119, pl. 6, fig. 67.

ECOLOGY.—Common in subtropical waters, neritic marine, benthic.

DISTRIBUTION.—Widespread but rare in Recent, most common in samples from Suisun Bay.

Genus and Species *indeterminate*
(Pl. 12, Fig. 12)

DESCRIPTION.—Valve triangular in outline, almost semilanceolate, asymmetrical, with one bluntly rounded angle and two strongly produced, subacute angles. Longest side 12–15 μm. All margins slightly concave. Valve surface punctate. Punctae large, round, in rows that follow the valve margin; 14–16 in 10 μm along the margin.

DISTRIBUTION.—Rare in the upper part of the Yerba Buena mud.

REMARKS.—This taxon is very similar to *Euodia barbadensis* Greville (1861), except for the protracted ends on the specimens described above. According to Van Landingham (1971), *Euodia* is not a valid genus and most species originally assigned to it were placed in *Hemidiscus* or *Triceratium*. However "*Euodia*" *barbadensis*, the type of the genus, was never reassigned. It is likely that neither "*Euodia barbadensis*" or this taxon belongs to *Hemidiscus* or *Triceratium*. This species and "*E. barbadensis*" may represent Grevilles original concept of '*Euodia*" or a new genus.

ACKNOWLEDGMENTS

This paper comprises a portion of a Ph.D. dissertation completed at the University of California, Berkeley under the direction of Drs. William Berry, Charlotte Brunner, and John West. I greatfully acknowledge their support and guid-

ance. I wish to thank the Estuarine Studies Group of the Water Resources Division of the U.S. Geological Survey at Menlo Park, California, especially Drs. John Conomos and Frederick Nicols for kindly allowing me to participate in the benthic sampling program aboard the RV ESTERO. Many people contributed their support, ideas, and expertise to this work, but at the risk of omitting someone I would like to especially thank Jack Baldauf, Al Mahood, Fred Nicols, Howard Schorn, Doris Sloan, Jan Thompson, Ray Wong, and Victor Zullo. I also thank Drs. John Barron and Hugh Gauch whose insightful reviews greatly improved the accuracy and clarity of the manuscript. Financial support for the project was provided by the Department of Paleontology, University of California, Berkeley.

Plate 1

FIGURE:

1. *Melosira moniliformis* (O. Müller) Agardh; scale bar equals 40 μm; with initial cell.
2. *Melosira moniliformis* (O. Müller) Agardh; L = 38 μm.
3. *Melosira moniliformis* (O. Müller) Agardh; L = 37 μm.
4. *Melosira moniliformis* (O. Müller) Agardh; L = 50 μm.
5. *Melosira moniliformis* (O. Müller) Agardh; D = 37 μm.
6. *Melosira moniliformis* (O. Müller) Agardh; L = 37 μm.
7. *Melosira nummuloides* (Dillw.) Agardh; L = 42 μm.
8. *Aulacosira ambigua* (Grunow) Simonsen; L = 12 μm.
9. *Aulacosira italica* (Ehrenberg) Simonsen; L = 17 μm.
10. *Aulacosira italica* (Ehrenberg) Simonsen; L = 31 μm.
11. *Aulacosira granulata* (Ehrenberg) Simonsen; L = 35 μm.
12. *Aulacosira granulata* (Ehrenberg) Simonsen; D = 24 μm.
13. *Aulacosira granulata* (Ehrenberg) Simonsen; D = 21 μm.
14. *Aulacosira granulata* (Ehrenberg) Simonsen; D = 21 μm. Same specimen as in Figure 13.
15. *Aulacosira granulata* (Ehrenberg) Simonsen; D = 25 μm.

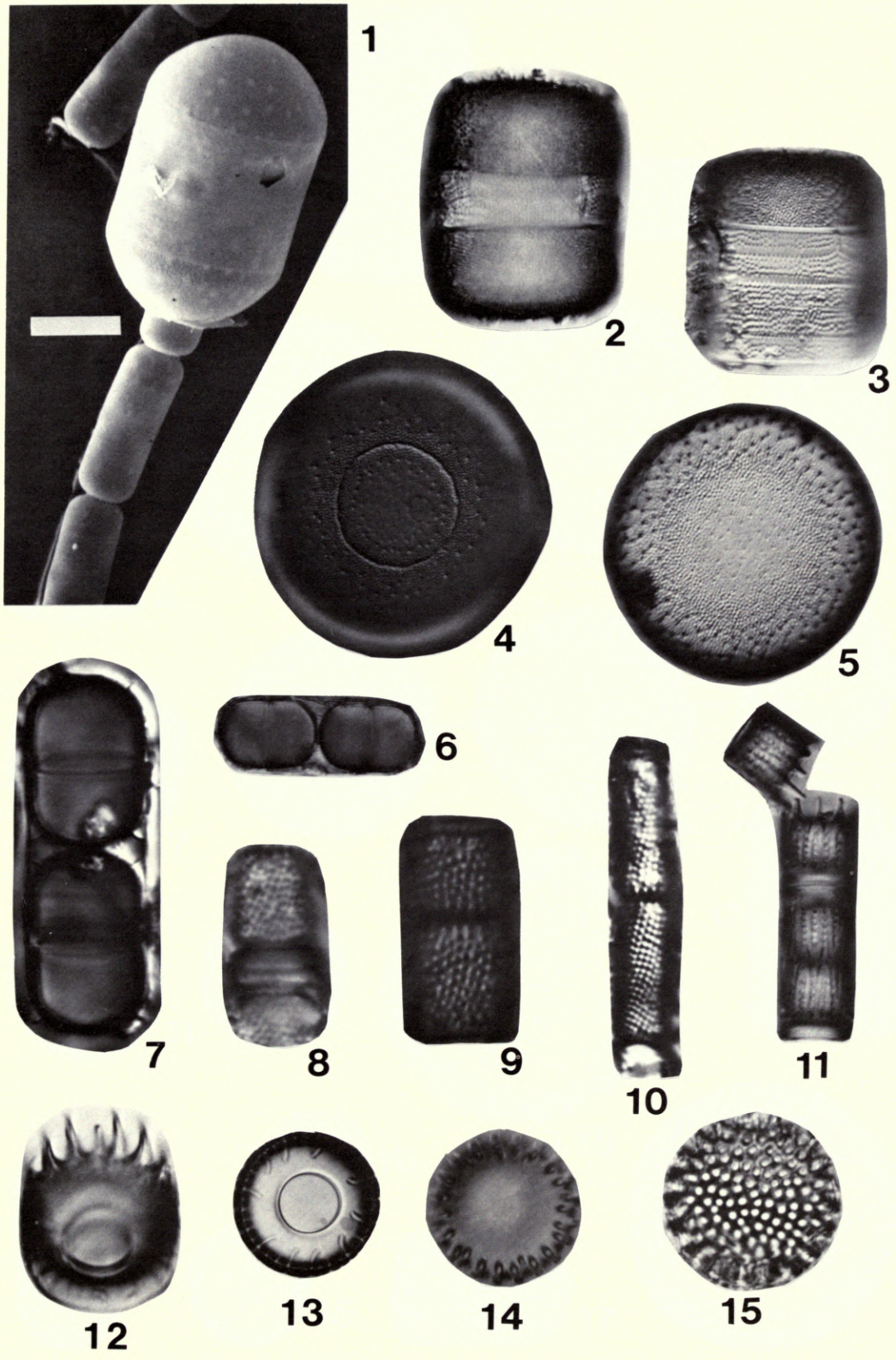

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

Plate 2

FIGURE:

1. *Melosira arenaria* Moore; D = 72 μm.
2. *Aulacosira islandica* (O. Müller) Simonsen; L = 28 μm.
3. *Aulacosira islandica* (O. Müller) Simonsen; L = 29 μm.
4. *Aulacosira islandica* (O. Müller) Simonsen; L = 30 μm.
5. *Paralia sulcata* (Ehrenberg) Cleve; D = 35 μm. a: focus down, b: focus up.
6. *Paralia sulcata* (Ehrenberg) Cleve; L = 60 μm.
7. *Paralia sulcata* (Ehrenberg) Cleve; D = 32 μm.
8. *Paralia sulcata* (Ehrenberg) Cleve; D = 39 μm.
9. *Paralia sulcata* (Ehrenberg) Cleve; D = 35 μm.
10. *Paralia sulcata* (Ehrenberg) Cleve; D = 38 μm.
11. *Paralia sulcata* (Ehrenberg) Cleve; D = 33 μm; a: upper valve of cell, b: lower valve of cell.
12. *Paralia sulcata* (Ehrenberg) Cleve; L = 45 μm.
13. *Paralia sulcata* (Ehrenberg) Cleve; D = 32 μm; a: focus up, b: focus down.
14. *Paralia sulcata* (Ehrenberg) Cleve; L = 28 μm.
15. *Paralia sulcata* (Ehrenberg) Cleve; D = 11 μm.
16. *Paralia sulcata* (Ehrenberg) Cleve; D = 11 μm.
17. *Paralia sulcata* (Ehrenberg) Cleve; L = 16 μm.

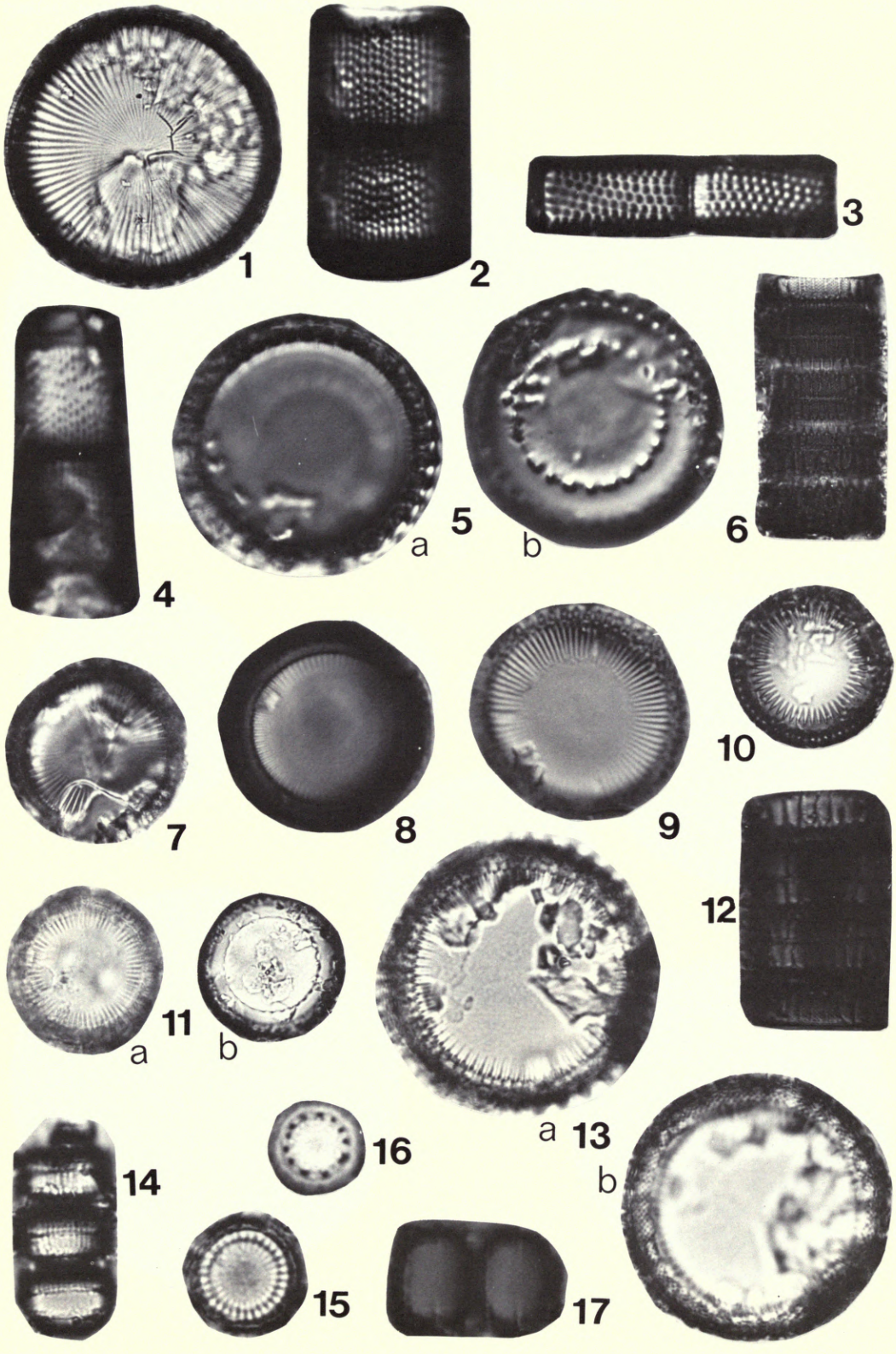

1
2
3
4
5
a
b
6
7
8
9
10
11
a
b
12
13
a
b
14
15
16
17

Plate 3

FIGURE:

1. *Cyclotella stelligera* Cleve; D = 8 μm.
2. *Cyclotella pygmaea* Pantocsek; D = 13 μm.
3. *Cyclotella comta* (Ehrenberg) Kutzing; D = 35 μm.
4. *Cyclotella striata* (Kutzing) Grunow; D = 20 μm.
5. *Cyclotella menegheniana* Kutzing; D = 10 μm.
6. *Cyclotella striata* (Kutzing) Grunow; D = 27 μm.
7. *Cyclotella stylorum* Brightwell; D = 38 μm.
8. *Cyclotella stylorum* Brightwell; D = 82 μm.
9. *Cyclotella stylorum* Brightwell; D = 50 μm.

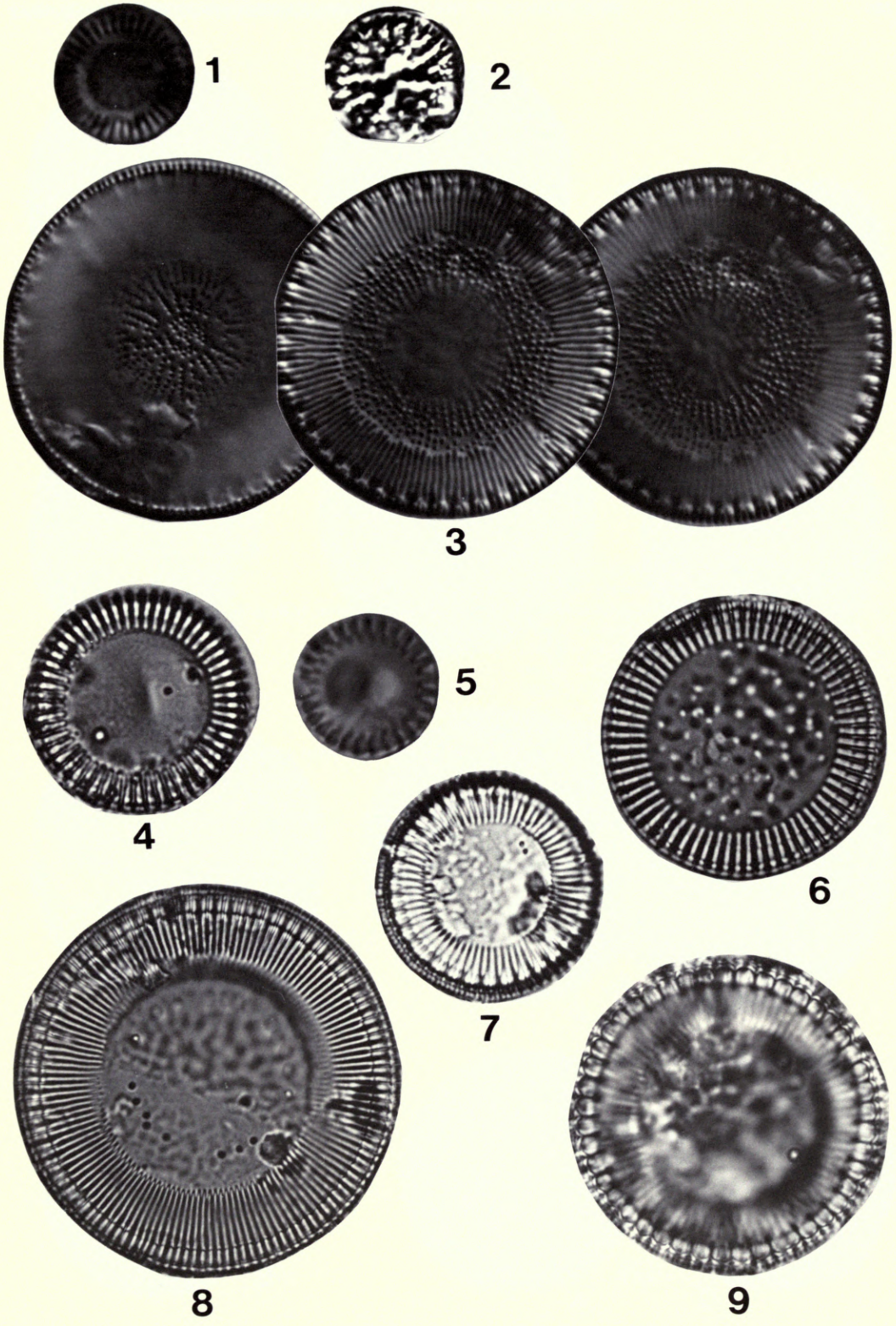

1
2
3
4
5
6
7
8
9

Plate 4

FIGURE:

1. *Stephanodiscus carconensis* Eulenstein *in* Grunow; D = 60 μm.
2. *Stephanodiscus carconensis* Eulenstein *in* Grunow; D = 20 μm.
3. *Stephanodiscus carconensis* Eulenstein *in* Grunow; D = 12 μm; a: focus down, b: focus up.
4. *Stephanodiscus carconensis* Eulenstein *in* Grunow; D = 36 μm.
5. *Stephanodiscus niagarae* Ehrenberg; D = 39 μm.
6. *Stephanodiscus niagarae* Ehrenberg; D = 48 μm.
7. *Stephanodiscus niagarae* Ehrenberg; D = 27 μm.
8. *Stephanodiscus niagarae* Ehrenberg; D = 61 μm; a, focus down, b, focus up.
9. *Stephanodiscus astrea* (Ehrenberg) Grunow; D = 22 μm.
10. *Stephanodiscus astrea* (Ehrenberg) Grunow; D = 19 μm; a, focus down, b, focus up.

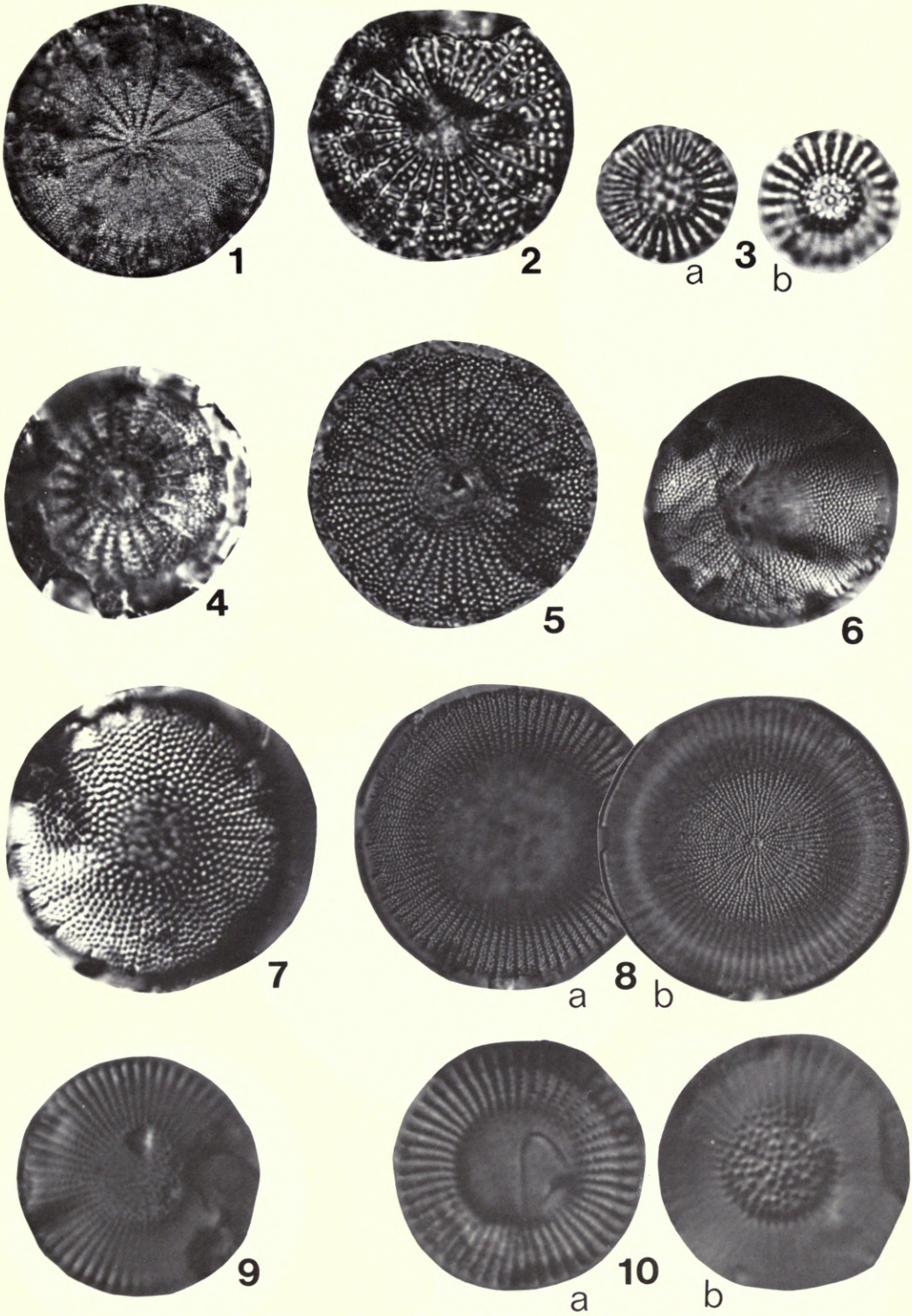

1
2
a
3
b
4
5
6
7
a
8
b
9
a
10
b

Plate 5

FIGURE:

1. *Coscinodiscus jonesianus* (Greville) Ostenfeld; scale bar is 20 μm.
2. *Coscinodiscus jonesianus* (Greville) Ostenfeld; D = 104 μm.
3. *Coscinodiscus decrescens* Grunow; D = 25 μm.
4. *Coscinodiscus oculus-iridis* Ehrenberg; D = 150 μm; a: central area and margin, b: entire valve.
5. *Coscinodiscus decrescens* Grunow; D = 19 μm.
6. *Coscinodiscus obscurus* Schmidt; D = 85 μm.
7. *Coscinodiscus radiatus* Ehrenberg; D = 35 μm.
8. *Coscinodiscus obscurus* Schmidt; D = 74 μm.
9. *Coscinodiscus obscurus* Schmidt; D = 85 μm; central area and margin of specimen in Figure 7.

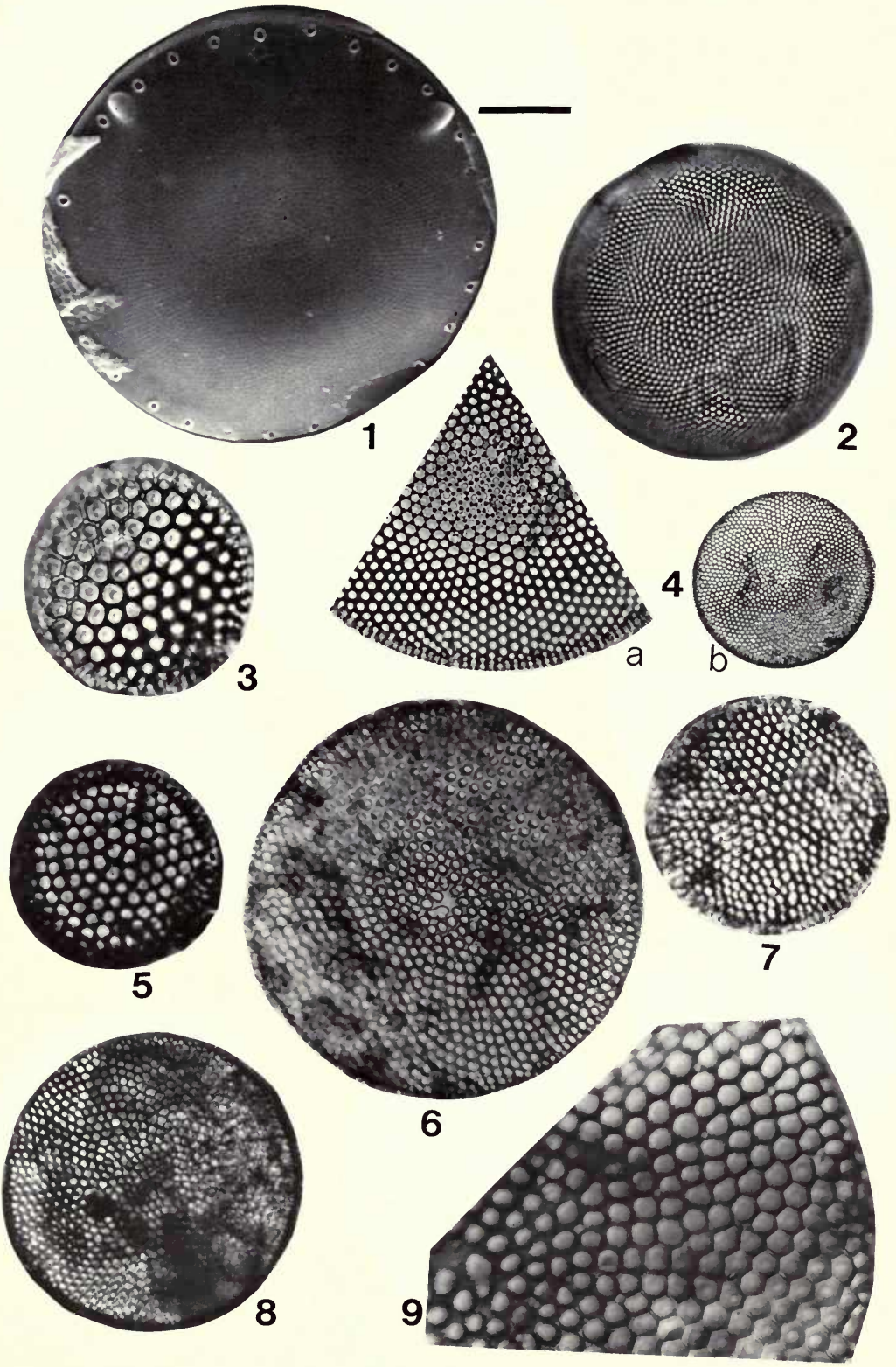

1
2
3
a
4
b
5
6
7
8
9

Plate 6

FIGURE:

1. *Coscinodiscus obscurus* Schmidt; D = 123 μm; a: entire valve, b: center area and margin.
2. *Coscinodiscus radiatus* Ehrenberg; D = 40 μm.
3. *Coscinodiscus radiatus* Ehrenberg; D = 64 μm.
4. *Coscinodiscus radiatus* Ehrenberg; D = 70 μm.
5. *Stephanopyxis*? sp.; D = 26 μm.
6. *Coscinodiscus marginatus* Ehrenberg; D = 26 μm; a: focus up, b: focus down.
7. *Thalassiosira lacustris* (Grunow) Hasle; D = 25 μm.
8. *Thalassiosira lacustris* (Grunow) Hasle; D = 37 μm; a: focus down, b: focus up.

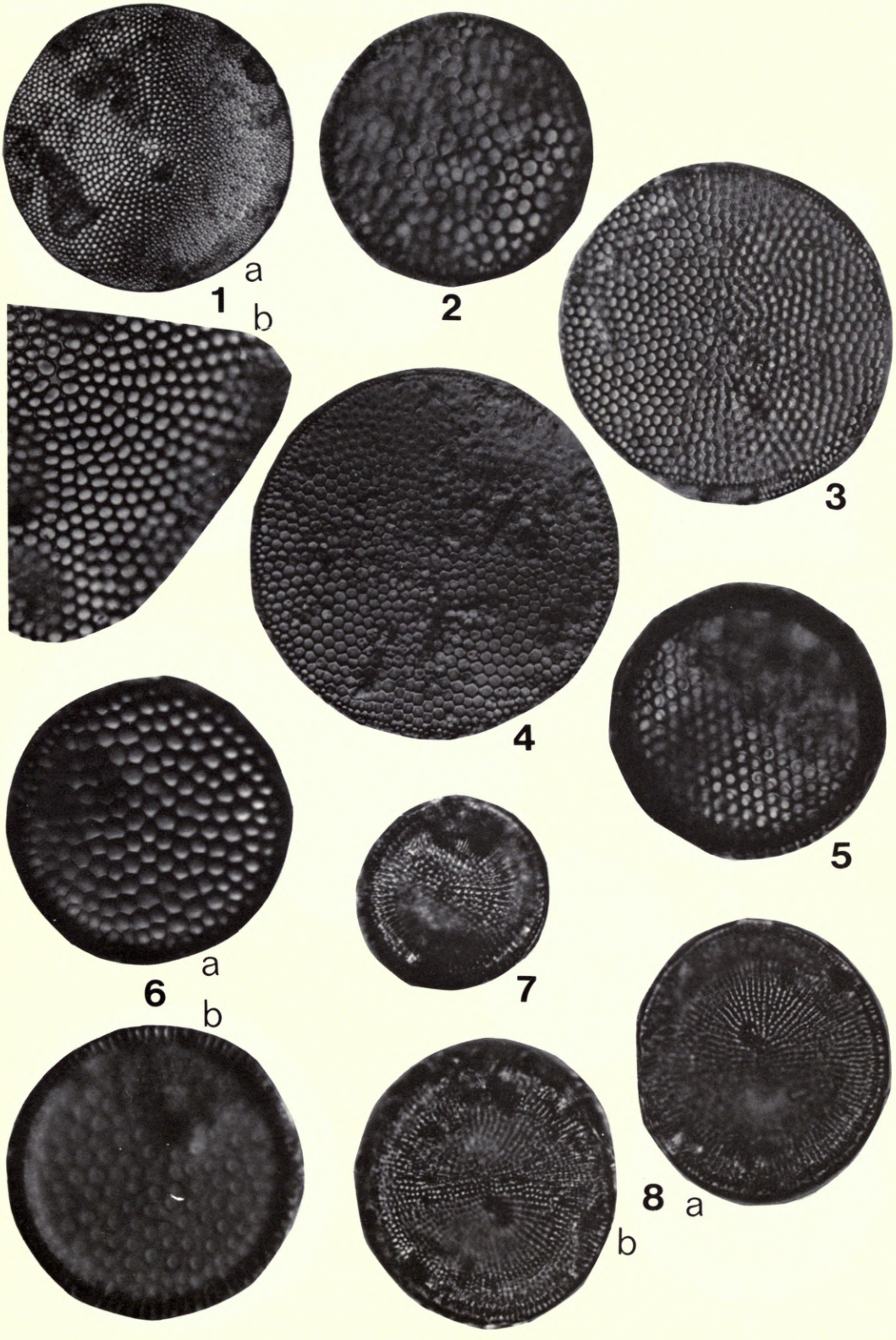

1 a
b
2
3
4
5
6 a
b
7
8 a
b

Plate 7

FIGURE:

1. *Thalassiosira lacustris* (Grunow) Hasle; D = 60 μm; a: focus up, b: focus down, c–f: margin showing tubular processes.
2. *Thalassiosira lacustris* (Grunow) Hasle; D = 29 μm.
3. *Coscinodiscus nitidus* Gregow; D = 25 μm.
4. *Cyclotella pygmaea* Pantocsek; D = 13 μm.
5. *Cyclotella striata* (Kutzing) Grunow; D = 32 μm.
6. *Cyclotella striata* (Kutzing) Grunow; D = 20 μm.
7. *Cyclotella comta* (Ehrenberg) Kutzing; D = 30 μm.

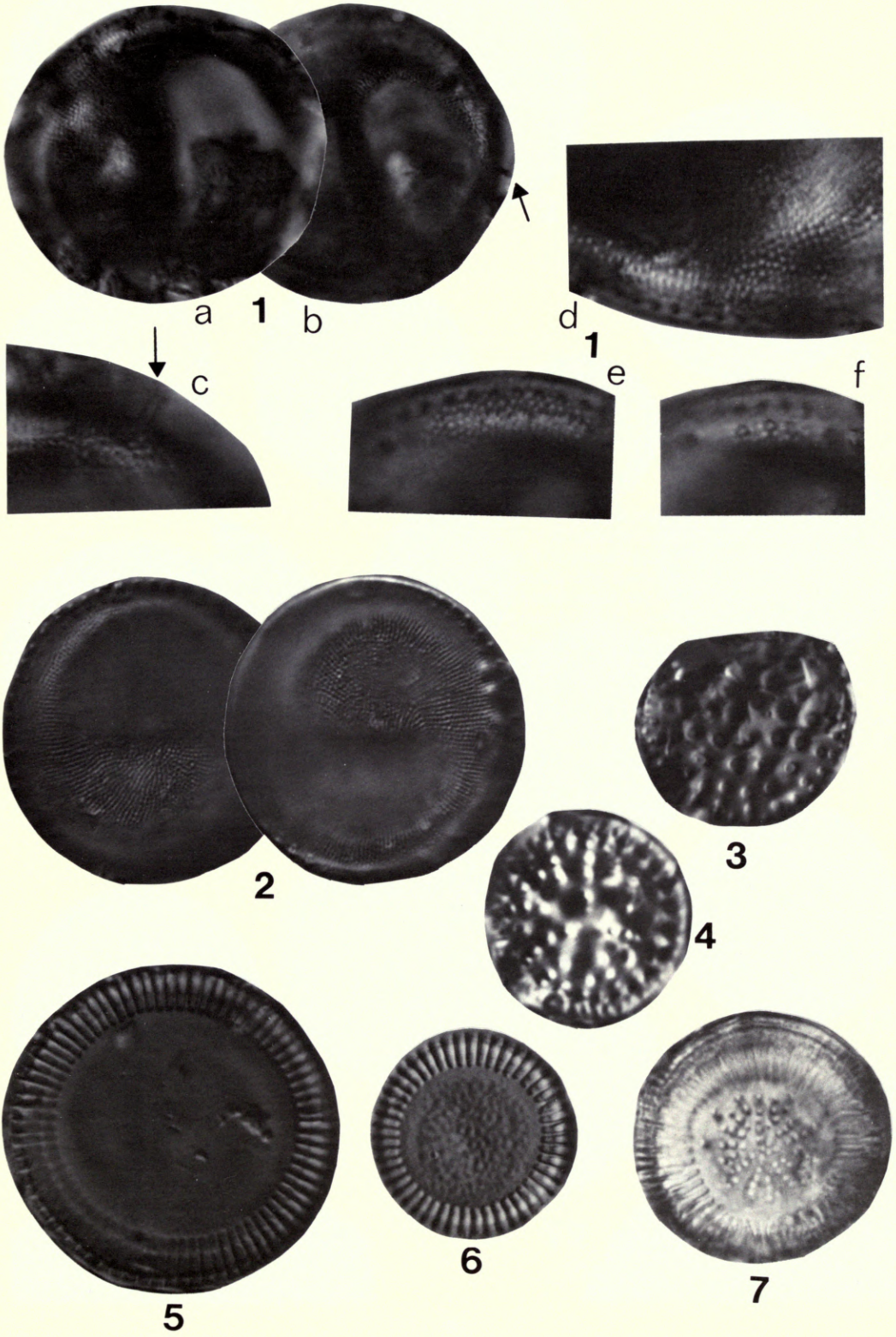

a
1
b
c
d
1
e
f
2
3
4
5
6
7

Plate 8

FIGURE:

1. *Actinocyclus normanii* (Gregory) Hustedt; D = 46 μm.
2. *Actinocyclus normanii* (Gregory) Hustedt; D = 43 μm.
3. *Actinocyclus normanii* (Gregory) Hustedt; D = 49 μm.
4. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 23 μm.
5. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 27 μm.
6. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 18 μm.
7. *Actinocyclus normanii* (Gregory) Hustedt; D = 45 μm.
8. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 17 μm.
9. *Actinocyclus normanii* (Gregory) Hustedt; D = 32 μm.
10. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 22 μm; arrow shows pseudonodule.
11. *Actinocyclus normanii* (Gregory) Hustedt; D = 44 μm.
12. *Actinocyclus normanii* (Gregory) Hustedt; D = 48 μm; a, b: focus down, shows pseudonodule(s)?; b: marginal focus, enlargement; c: entire valve, focus down; d: focus up; e: focus down, marginal focus, shows striate margin.

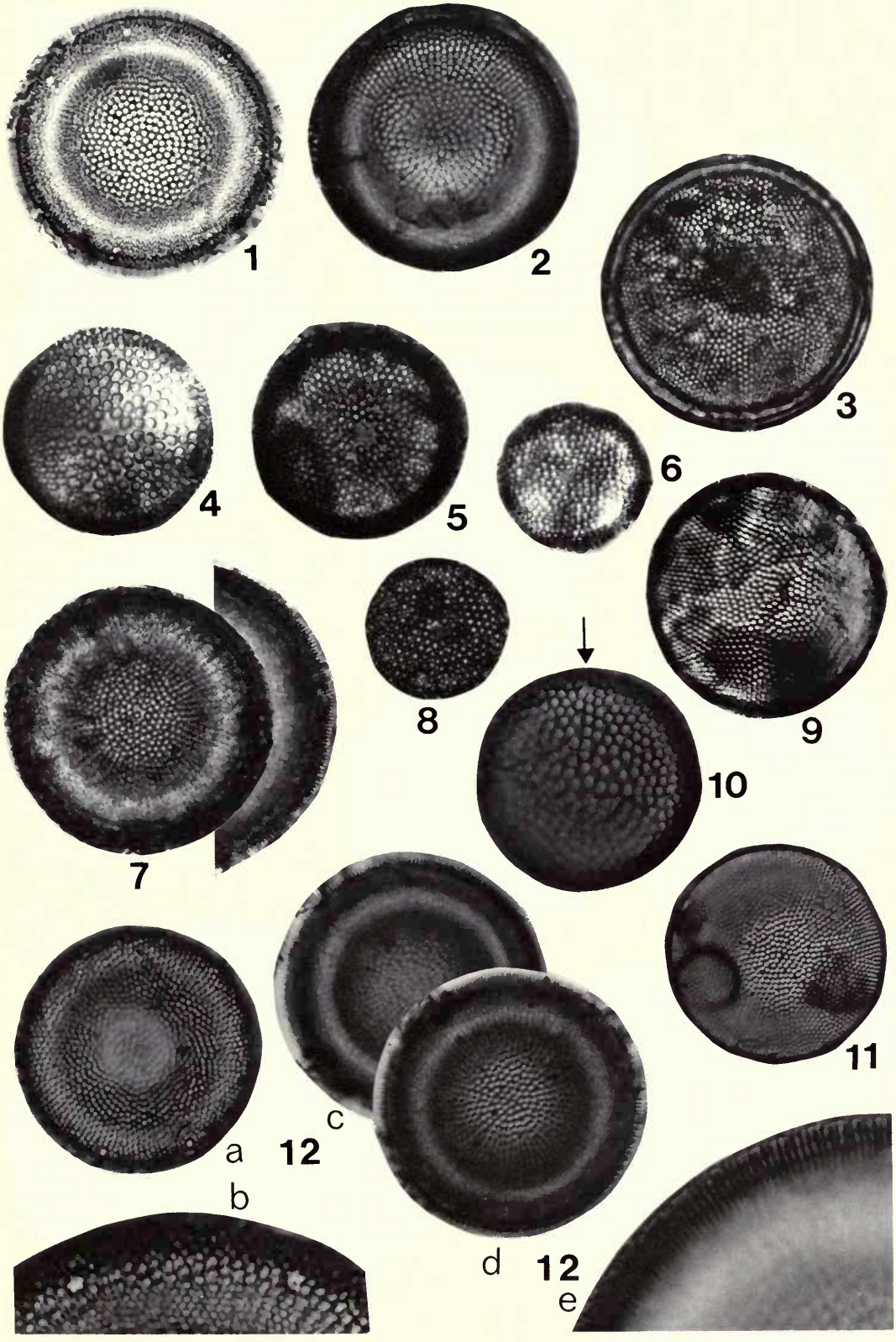

1
2
3
4
5
6
7
8
9
10
11
a
12
b
c
d
12
e

Plate 9

FIGURE:

1. *Actinocyclus octanarius* Ehrenberg; D = 72 μm; a: marginal enlargement, b: entire valve; c: dark field.
2. *Actinocyclus*? sp. 1; D = 28 μm.
3. *Coscinodiscus curvatulus* Grunow; D = 64 μm.
4. *Coscinodiscus curvatulus* Grunow; D = 88 μm.
5. *Actinocyclus octanarius* Ehrenberg; D = 96 μm.
6. *Thalassiosira* sp. 1; D = 26 μm; a: focus down, b: focus up.
7. *Thalassiosira punctigera* (Castracane) Hasle; D = 85 μm.
8. *Thalassiosira punctigera* (Castracane) Hasle; D = 115 μm.

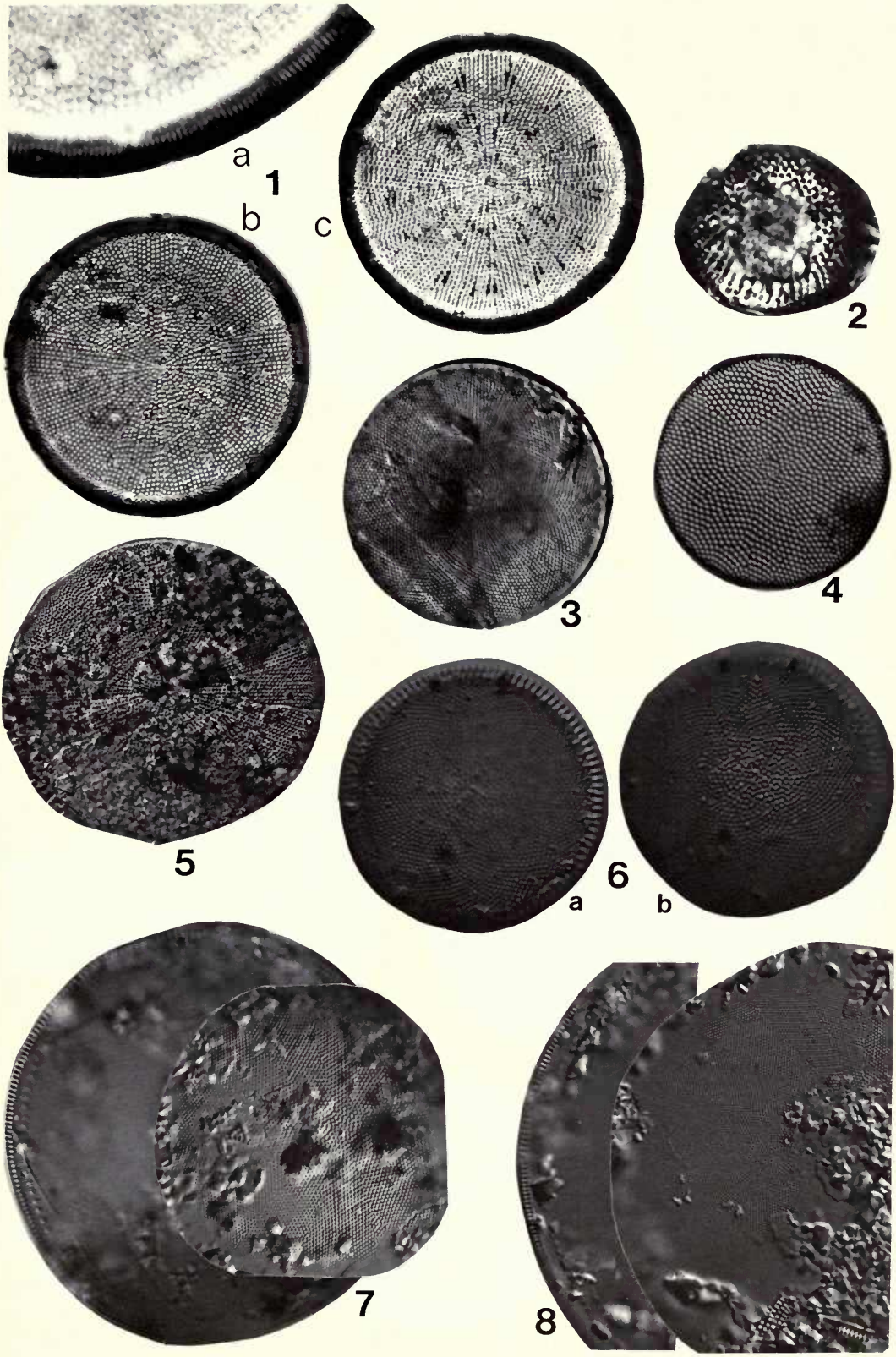

a
1
b
c
2
3
4
5
6
a
b
7
8

Plate 10

FIGURE:

1. *Thalassiosira nodulolineata* (Hendey) Hasle and Fryxell; D = 50 μm; a: entire valve, b: central area and marginal enlargement, c: focus down, d: dark field.
2. *Thalassiosira hendeyi* Hasle and Fryxell; D = 68 μm; a: entire valve, b: central area and marginal enlargement, arrows show processes.
3. *Thalassiosira hendeyi* Hasle and Fryxell; D = 30 μm.
4. *Thalassiosira hendeyi* Hasle and Fryxell; D = 27 μm; a: focus down, b: focus up.
5. *Thalassiosira hendeyi* Hasle and Fryxell; D = 28 μm.
6. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 46 μm.
7. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 48 μm.

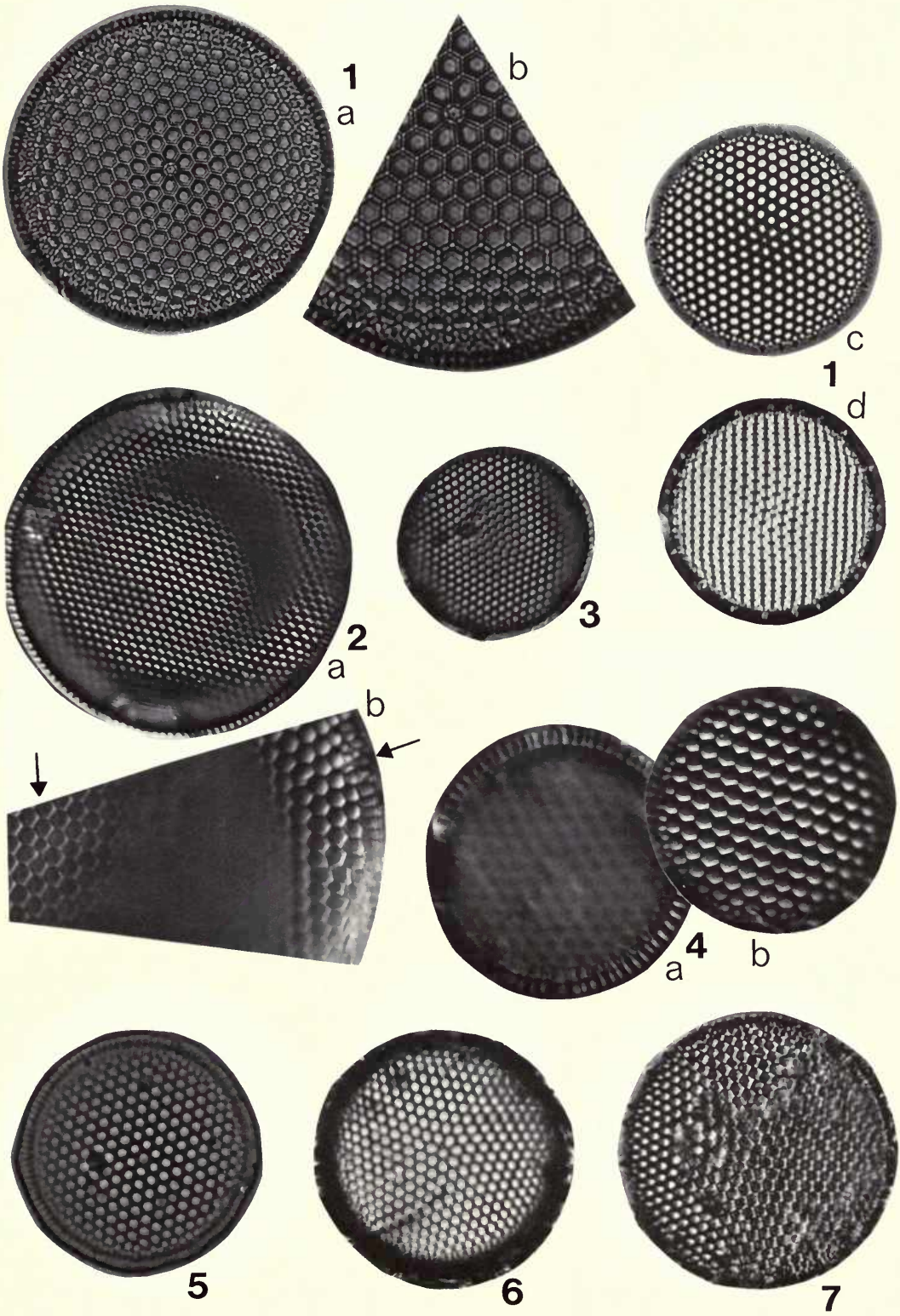

1
a
b
c
1
d
2
a
3
b
4
a
b
5
6
7

Plate 11

FIGURE:

1. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 40 μm.
2. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 33 μm.
3. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 45 μm.
4. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 66 μm; a: entire valve, b: central area and marginal enlargement.
5. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 42 μm; a: entire valve, b: central area and marginal enlargement, note tubular process at 3 o'clock.
6. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 36 μm.
7. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 53 μm.
8. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 34 μm.
9. *Thalassiosira* cf. *T. pacifica* Gran and Angst; D = 72 μm.

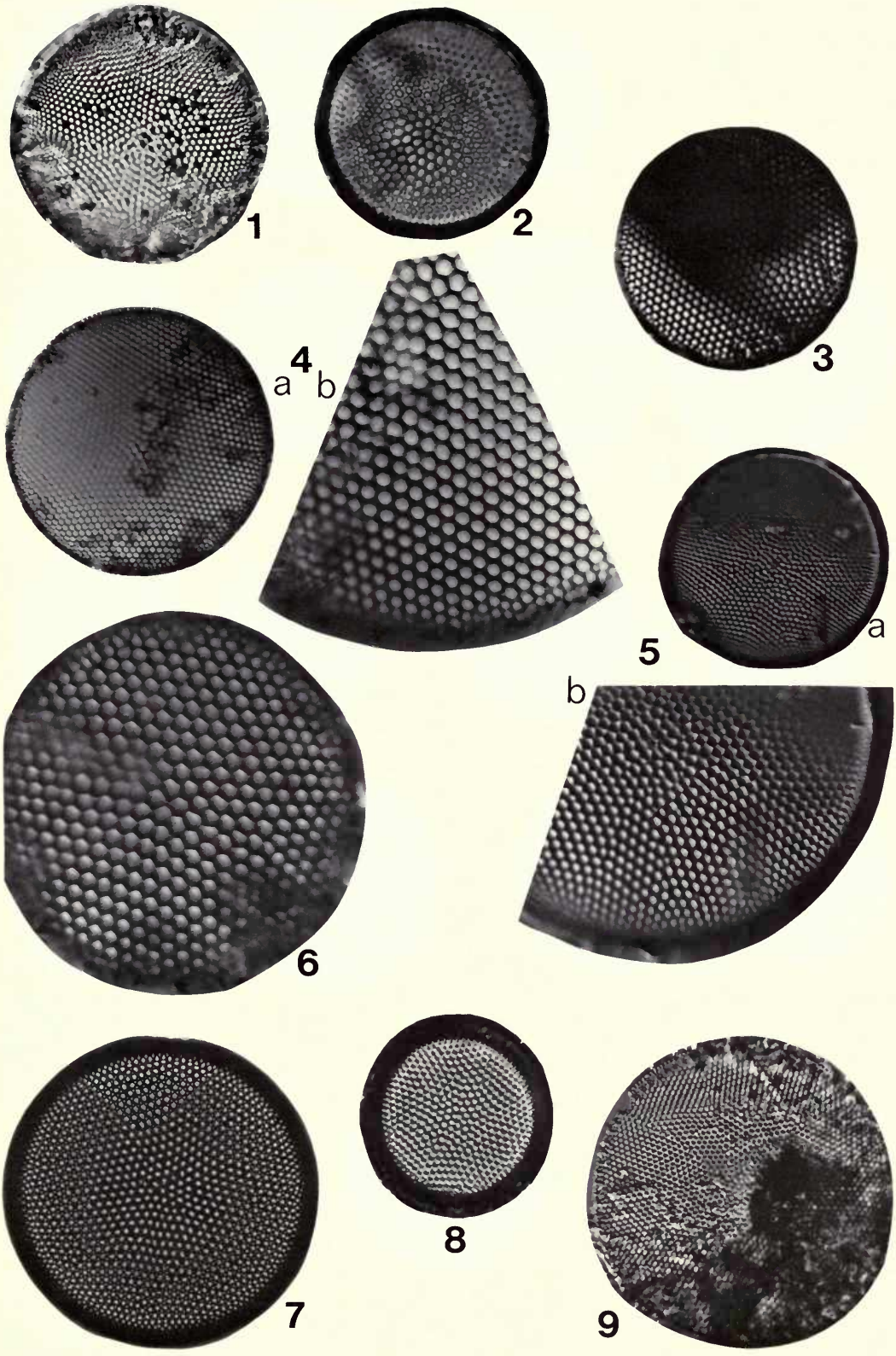

1
2
3
4
a
b
5
a
b
6
7
8
9

Plate 12

FIGURE:

1. *Thalassiosira decipiens* (Grunow) Jorgensen; D = 32 μm; a: focus up, b: focus down.
2. *Thalassiosira decipiens* (Grunow) Jorgensen; D = 27 μm.
3. *Thalassiosira decipiens* (Grunow) Jorgensen; D = 40 μm; a, focus up, b, focus down.
4. *Thalassiosira decipiens* (Grunow) Jorgensen; D = 21 μm; a: focus down, b: focus up.
5. *Thalassiosira decipiens* var. 1; D = 14 μm; a: focus down, b: focus up.
6. *Thalassiosira decipiens* var. 1; D = 16 μm.
7. *Thalassiosira decipiens* var. 1; D = 11 μm.
8. *Thalassiosira decipiens* var. 1; D = 15 μm; a: focus down, b: focus up.
9. *Thalassiosira decipiens* var. 1; D = 14 μm; a: focus down, b: focus up.
10. *Hyalodiscus scoticus* (Kutzing) Grunow; D = 96 μm.
11. *Hyalodiscus scoticus* (Kutzing) Grunow; D = 88 μm.
12. Genus and species indeterminate; L = 15 μm.

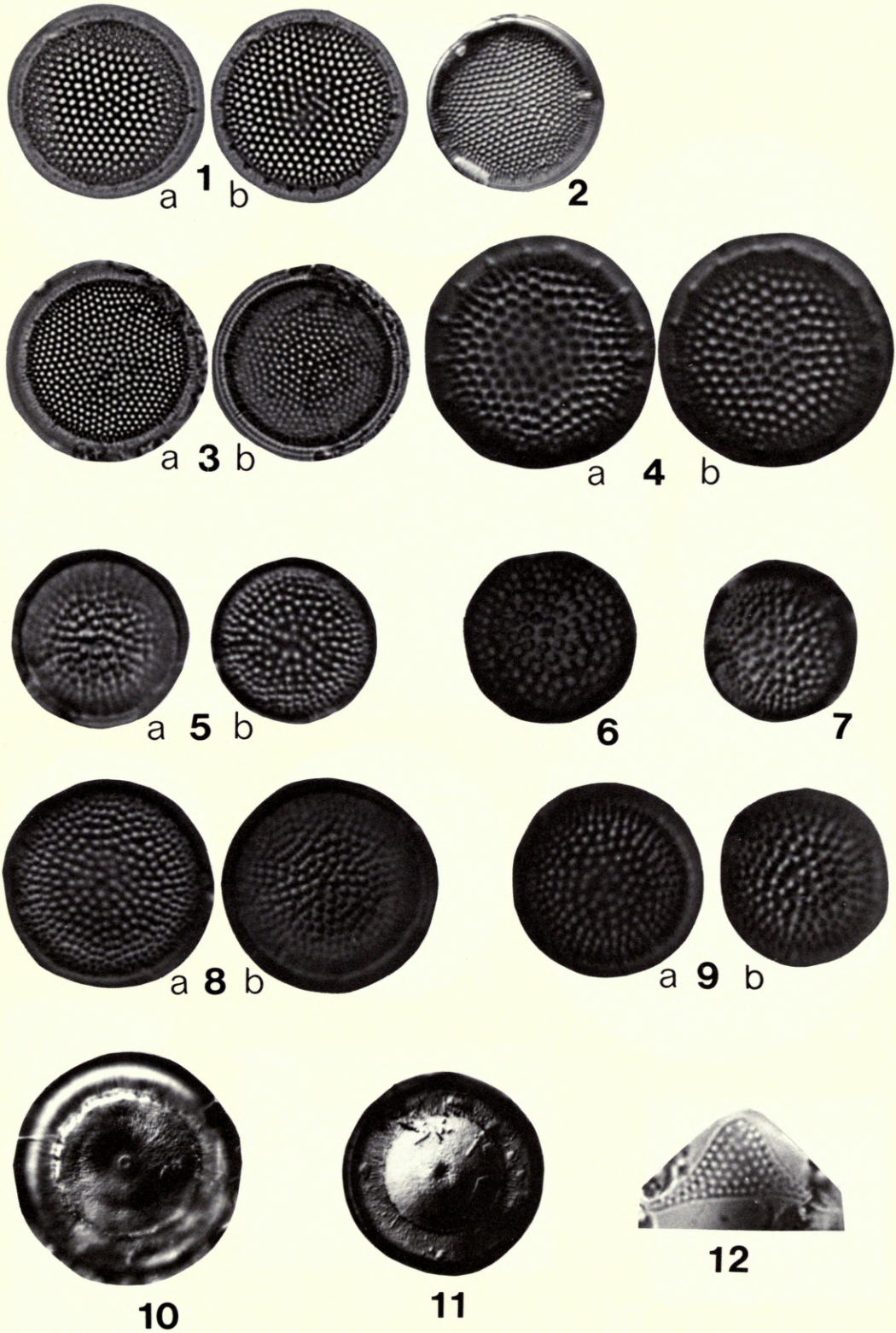
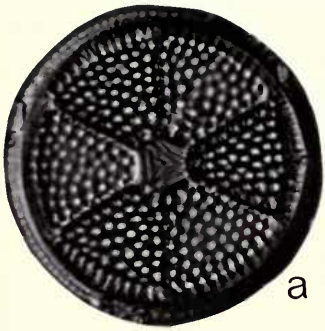

a 1 b
2
a 3 b
a 4 b
a 5 b
6
7
a 8 b
a 9 b
10
11
12

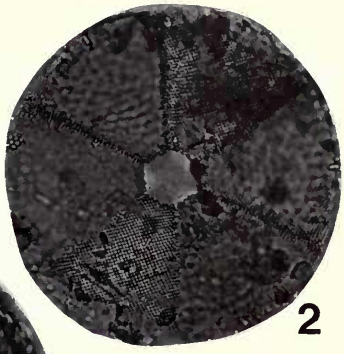
Plate 13

FIGURE:

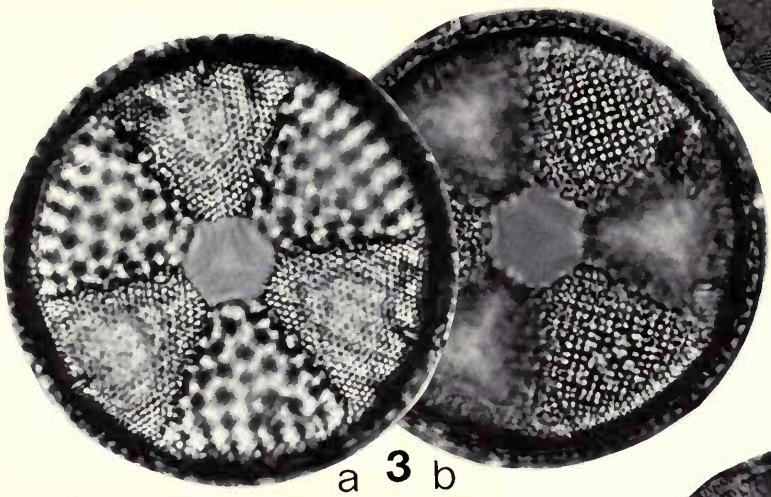
1. *Actinoptychus senarius* Ehrenberg; D = 86 μm; a: bright field, b: dark field.
2. *Actinoptychus senarius* Ehrenberg; D = 96 μm.
3. *Actinoptychus senarius* Ehrenberg; D = 77 μm; a: focus up, b: focus down.
4. *Actinoptychus senarius* Ehrenberg; D = 60 μm.
5. *Actinoptychus splendens* (Shadbolt) Ralfs; D = 21 μm.
6. *Actinoptychus splendens* (Shadbolt) Ralfs; D = 40 μm.
7. *Actinoptychus senarius* Ehrenberg; D = 76 μm; "Debya insignis," Auxospore of *A. senarius.*
8. *Biddulphia aurita* (Lyngbye) Brébisson; L = 64 μm.
9. *Biddulphia aurita* (Lyngbye) Brébisson; L = 68 μm.
10. *Biddulphia aurita* (Lyngbye) Brébisson; L = 42 μm.



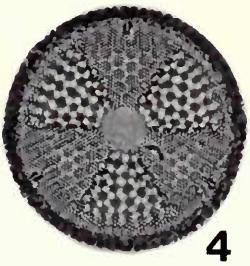
a 1 b



2

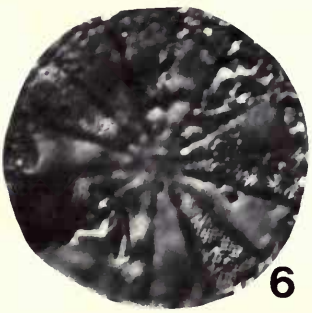


a 3 b



4

5



6

7

8

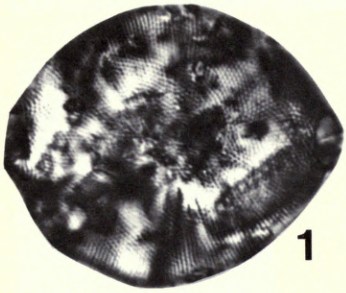
9

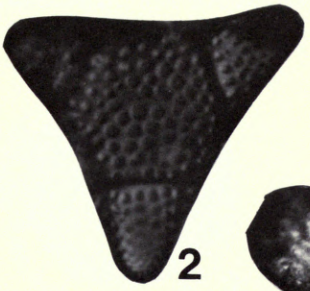
10

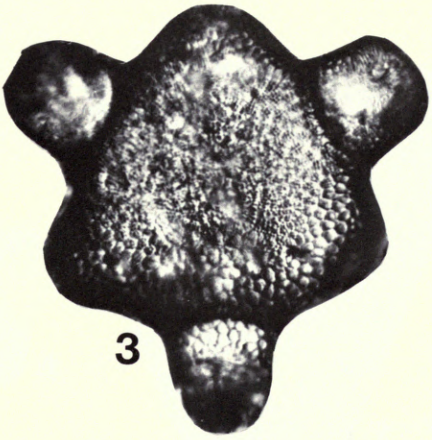
Plate 14

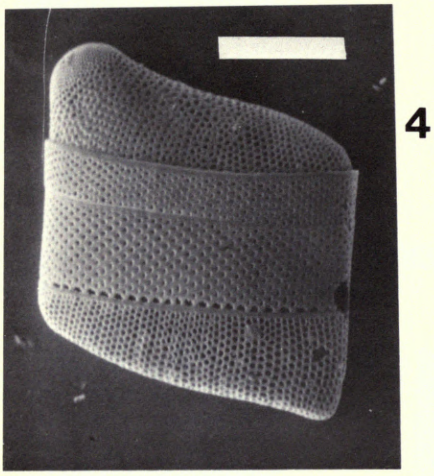
FIGURE:

1. *Biddulphia laevis* Ehrenberg; L = 51 μm.
2. *Biddulphia alternas* (Bailey) Van Heurck; L = 27 μm.
3. *Hydrosera triquetra* Wallich; L = 72 μm.
4. *Isthmia nervosa* Kutzing; Scale bar is 100 μm.
5. *Arachnoidiscus ehrenbergii* Bailey; Scale bar is 40 μm.
6. *Terpsinoe americana* (Bailey) Ralfs *in* Pritchard; L = 56 μm.
7. *Terpsinoe americana* (Bailey) Ralfs *in* Pritchard; L = 48 μm; girdle view.
8. *Triceratium dubium* Brightwell; L = 39 μm.
9. *Rhizosolenia* sp. 1; L = 120 μm.
10. *Cerataulus turgidus* (Ehrenberg) Ehrenberg; L = 64 μm.

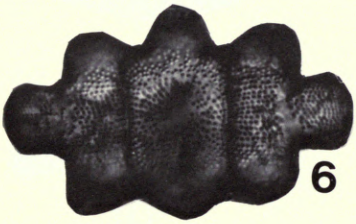

1

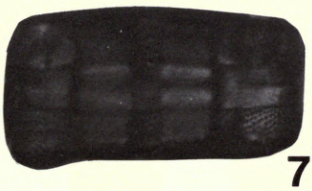

2

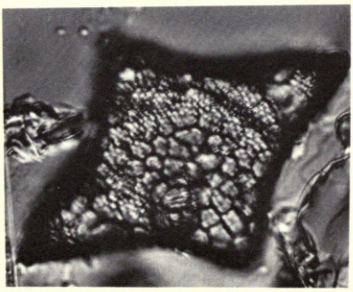

3


4

5


6


7


8

9

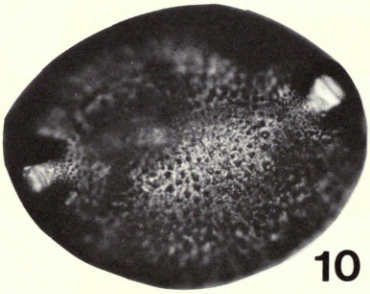

10

Plate 15

FIGURE:

1. *Chaetoceros cinctus* Gran; L = 26 μm.
2. *Chaetoceros* sp. 1; D = 16 μm.
3. *Chaetoceros*? sp. 2; L = 73 μm (of each spine).
4. *Chaetoceros mitra* (Bailey) Cleve; L = 20 μm.
5. *Ditylum brightwellii* (West) Grunow *in* Van Heurck; L = 80 μm.
6. *Ditylum brightwellii* (West) Grunow *in* Van Heurck; D = 48 μm.
7. *Cymatosira belgica* Grunow *in* Van Heurck; L = 14 μm; a: dark field, b: bright field, girdle view.
8. *Cymatosira belgica* Grunow *in* Van Heurck; L = 17 μm.
9. *Cymatosira belgica* Grunow *in* Van Heurck; L = 35 μm.
10. *Eunotogramma marina* (Smith) Peragallo; L = 21 μm.
11. *Diatoma vulgare* var. *breve* Grunow; L = 22 μm.
12. *Diatoma anceps* (Ehrenberg) Kirchn. *in* Cohn; L = 19 μm.
13. *Cymatosira belgica* Grunow; L = 14 μm; girdle view.
14. *Grammatophora marina* (Lyngbye) Kutzing; L = 36 μm.
15. *Dimeregramma minor* (Gregory) Ralfs; L = 48 μm.
16. *Dimeregramma minor* (Gregory) Ralfs; L = 48 μm.
17. *Grammatophora marina* (Lyngbye) Kutzing; L = 35 μm.
18. *Grammatophora marina* (Lyngbye) Kutzing; L = 27 μm.

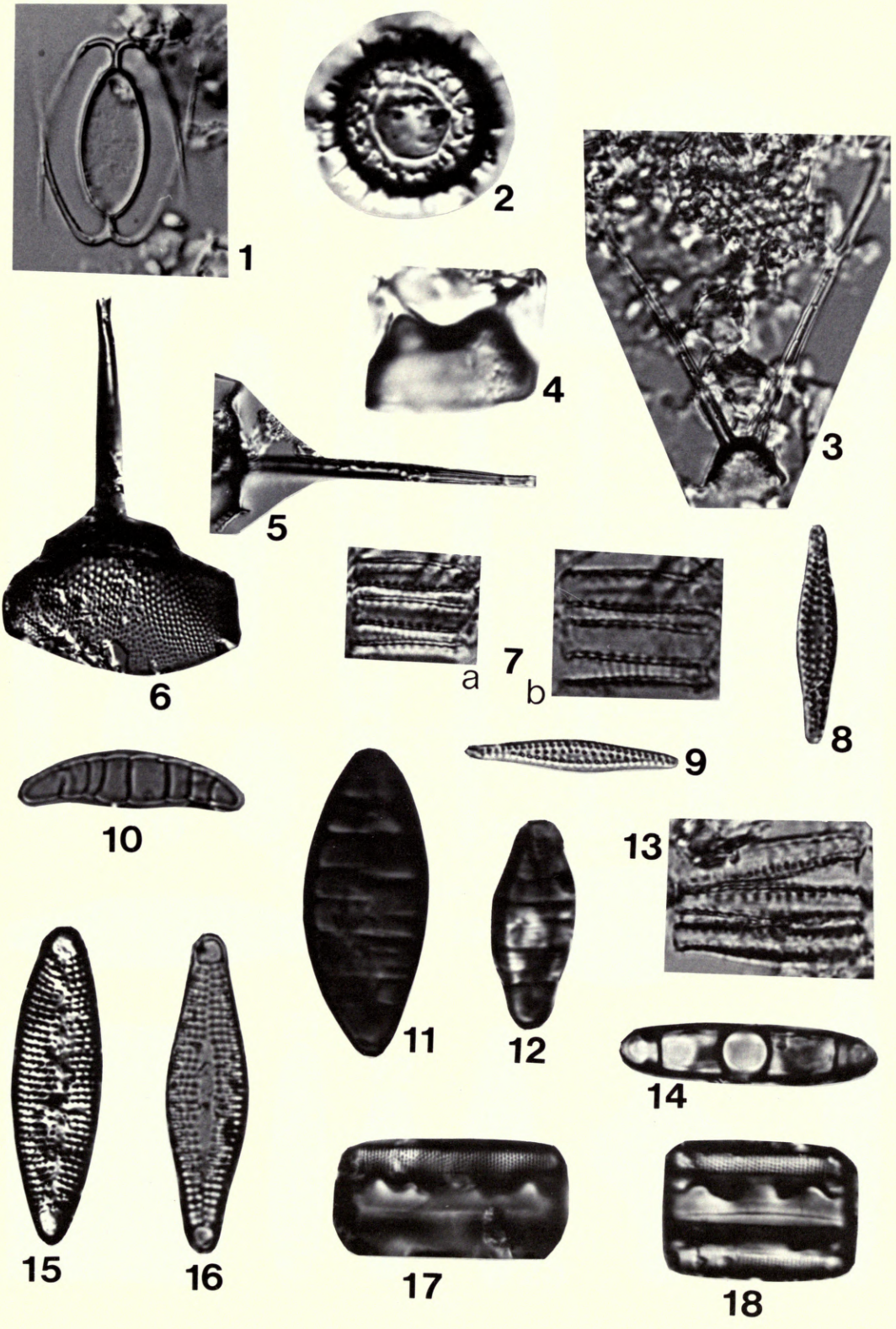

1
2
3
4
5
6
7
a
b
8
9
10
11
12
13
14
15
16
17
18

Plate 16

FIGURE:

1. *Opephora swartzii* (Grunow) Petit; L = 25 μm.
2. *Opephora swartzii* (Grunow) Petit; L = 14 μm.
3. *Ophephora pacifica* (Grunow) Petit; L = 29 μm.
4. *Meridion circulare* var. *constrictum* (Ralfs) Van Heurck; L = 28 μm.
5. *Rhabdonema arcuatum* (Agardh) Kutzing; L = 53 μm.
6. *Rhaphoneis amphiceros* (Ehrenberg) Ehrenberg; L = 35 μm.
7. *Rhaphoneis margaritalimbata* Mertz; L = 10 μm.
8. *Rhaphoneis surirella* (Ehrenberg) Grunow; L = 40 μm.
9. *Thalassionema nitzschioides* Hustedt; L = 74 μm.
10. *Tabellaria fenestra* (Lyngbye) Kutzing; L = 97 μm.
11. *Trachysphenia acuminata* Peragallo?; L = 29 μm.
12. *Fragilaria construens* var. *venter* (Ehrenberg) Grun.; L = 10 μm.
13. *Fragilaria tabulata* (Agardh) Lange-Bertalot; L = 82 μm.
14. *Fragilaria capucina* Desmazieres; L = 48 μm.
15. *Fragilaria crotonensis* Kitton; L = 88 μm.
16. *Fragilaria ulna* (Nitzsch) Lange-Bertalot; L = 96 μm.
17. *Fragilaria ulna* (Nitzsch) Lange-Bertalot; L = 187 μm; shown in two halves with central area for reference.
18. *Fragilaria construens* var. *binodis* (Ehrenberg) Grunow; L = 23 μm.
19. *Fragilaria virescens* var. *elliptica* Hustedt; L = 15 μm.
20. *Fragilaria construens* (Ehrenberg) Grunow; L = 24 μm.
21. *Fragilaria lapponica* Grunow; L = 15 μm.
22. *Fragilaria construens* var. *pumilla* Grunow; L = 12 μm.
23. *Fragilaria brevistriata* Grunow *in* Van Heurck; L = 21 μm.
24. *Fragilaria leptostauron* (Ehrenberg) Hustedt; L = 21 μm.
25. *Fragilaria capucina* var. *vaucheriae* (Kutzing) Lange-Bertalot; L = 27 μm.

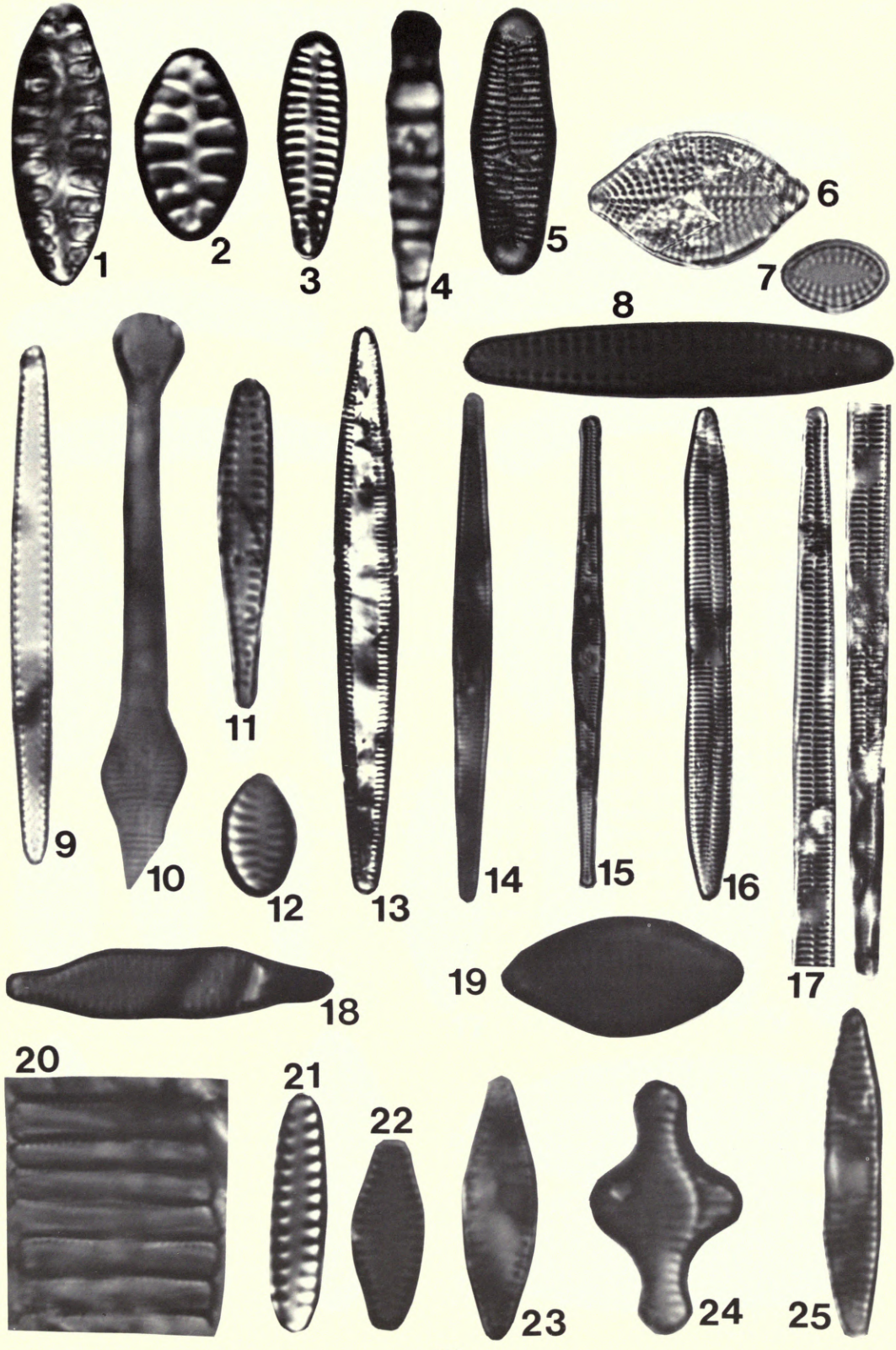

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

Plate 17

FIGURE:

1. *Eunotia eruca* Ehrenberg; L = 77 μm.
2. *Eunotia eruca* Ehrenberg; L = 27 μm.
3. *Eunotia eruca* Ehrenberg; L = 34 μm.
4. *Eunotia arcus* Ehrenberg; L = 25 μm.
5. *Eunotia monodon* Ehrenberg; L = 62 μm.
6. *Eunotia arcus* var. *bidens* (Ehrenberg) Grunow; L = 50 μm.
7. *Eunotia monodon* Ehrenberg; L = 52 μm.
8. *Eunotia triodon* Ehrenberg; L = 32 μm.
9. *Achnanthes conspicua* var. *brevistriata* Hustedt; L = 24 μm.
10. *Achnanthes wellsiae* Reimer; L = 16 μm; a: RV focus up, b: PRV focus down.
11. *Achnanthes haukiana* var. *rostrata* Schulz; L = 12 μm.
12. *Achnanthes haukiana* var. *rostrata* Schulz; L = 10 μm.
13. *Achnanthes haukiana* var. *rostrata* Schulz; L = 16 μm.
14. *Achnanthes haukiana* Grunow; L = 8 μm.
15. *Achnanthes haukiana* var. *rostrata* Schulz; L = 10 μm.
16. *Achnanthes groenlandica* var. *phinneyi* McIntire and Reimer; L = 18 μm.
17. *Achnanthes brevipes* var. *intermedia* (Kutzing) Cleve; L = 38 μm.
18. *Achnanthes brevipes* var. *intermedia* (Kutzing) Cleve; L = 62 μm.
19. *Achnanthes brevipes* var. *intermedia* (Kutzing) Cleve; L = 43 μm; a: RV focus up, b: PRV focus down.
20. *Achnanthes lanceolata* Brébisson *in* Kutzing; L = 15 μm.
21. *Achnanthes lanceolata* Brébisson *in* Kutzing; L = 11 μm.
22. *Achnanthes brevipes* Agardh; L = 47 μm.
23. *Achnanthes longipes* Agardh; L = 52 μm; a: focus up, b: focus down.

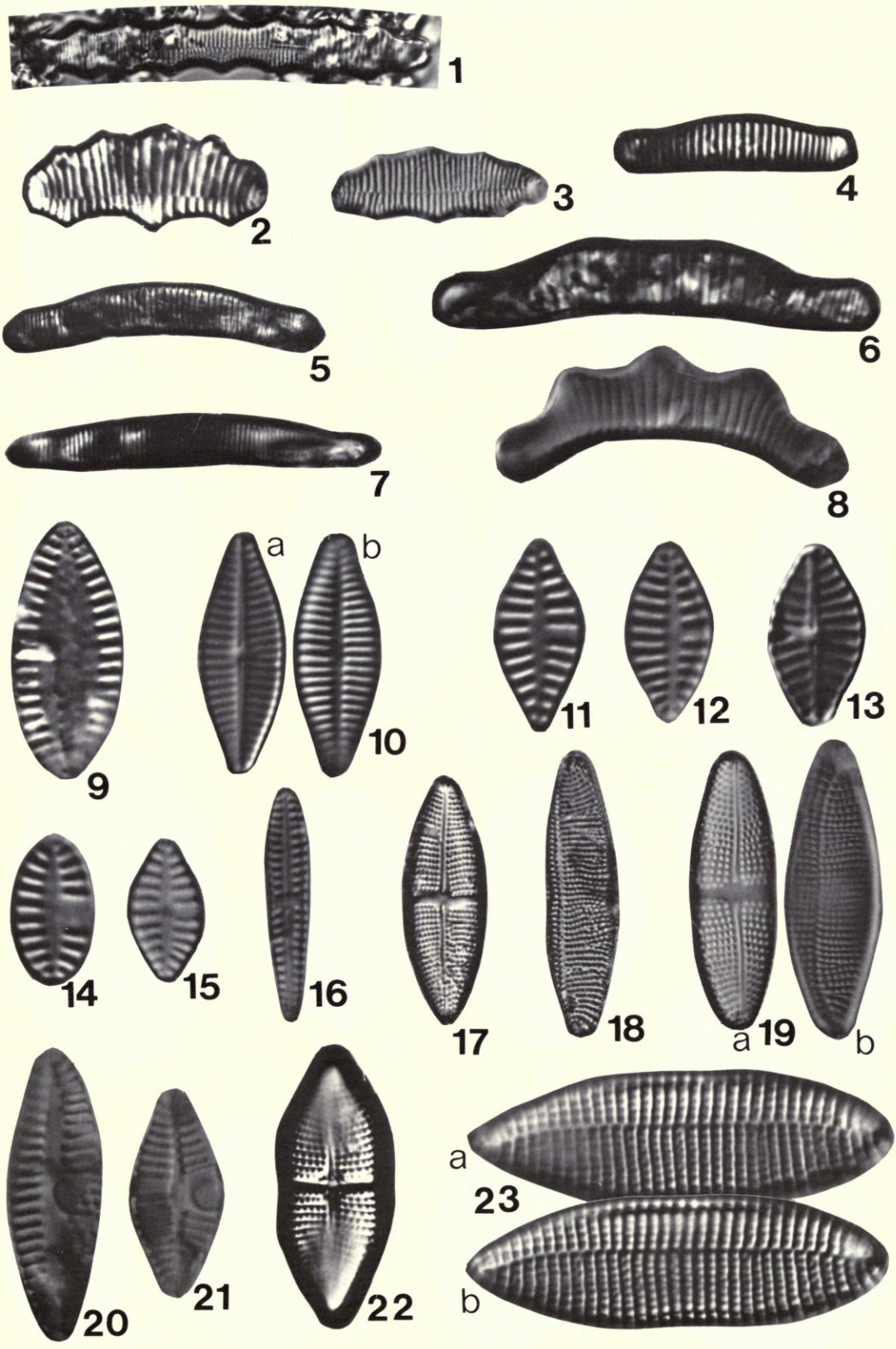

1
2
3
4
5
6
7
8
9
a
b
10
11
12
13
14
15
16
17
18
a
19
b
20
21
22
a
23
b

Plate 18

FIGURE:

1. *Achnanthes yaquinensis* McIntire and Reimer; L = 37 μm.
2. *Achnanthes parvula* Kutzing; L = 31 μm; a: RV focus up, b: PRV focus down.
3. *Achnanthes wellsiae* Reimer?; L = 16 μm; a: RV focus up, b: PRV focus down.
4. *Cocconeis scutellum* Ehrenberg; L = 25 μm.
5. *Cocconeis placentula* Ehrenberg; L = 24 μm; a: central area, focus up, b: margin focus down.
6. *Cocconeis placentula* Ehrenberg; L = 30 μm.
7. *Cocconeis vitrea* Brun; L = 41 μm.
8. *Cocconeis vitrea* Brun; L = 44 μm.
9. *Cocconeis vitrea* Brun; L = 26 μm.
10. *Cocconeis diminuta* Pantocsek; L = 13 μm.
11. *Cocconeis diminuta* Pantocsek; L = 11 μm.
12. *Cocconeis diminuta* Pantocsek; L = 15 μm.
13. *Cocconeis californica* (Grunow) Cleve; L = 19 μm.
14. *Cocconeis californica* (Grunow) Cleve; L = 19 μm.
15. *Cocconeis decipiens* Cleve; L = 40 μm.
16. *Cocconeis* sp. 1; L = 19 μm.

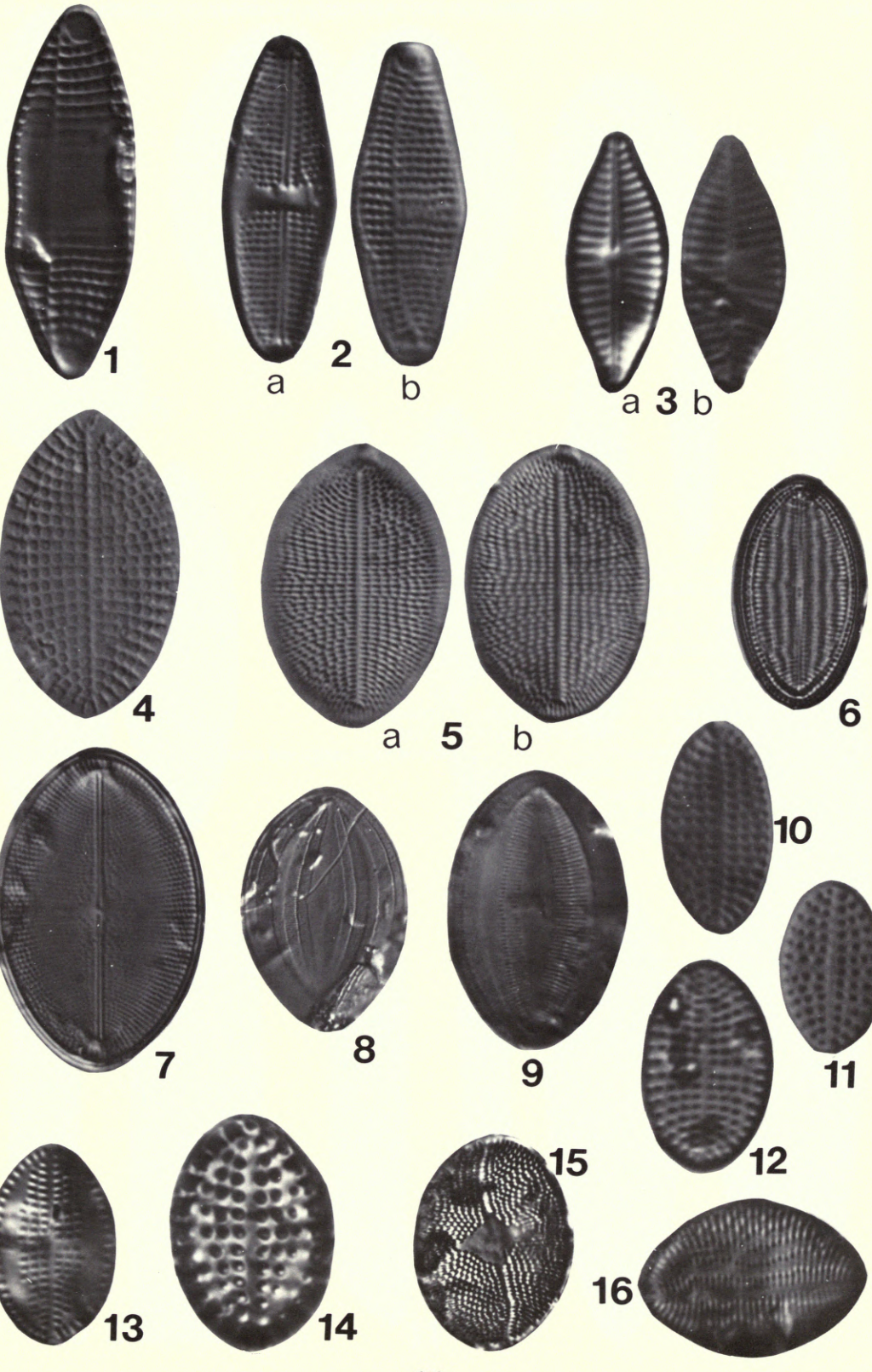

1
2
a
b
3
a
b
4
5
a
b
6
7
8
9
10
11
12
13
14
15
16

Plate 19

FIGURE:

1. *Cocconeis fasciolata* Ehrenberg; L = 26 μm.
2. *Cocconeis fasciolata* Ehrenberg; L = 29 μm; a: focus up, b: focus down.
3. *Cocconeis* sp. 2; L = 15 μm.
4. *Amphipleura rutilans* (Trent.) Cleve; L = 30 μm.
5. *Cocconeis scutellum* Ehrenberg?; L = 24 μm.
6. *Rhoicosphenia curvata* (Kutzing) Grun. *in* Rabenhorst; L = 29 μm.
7. *Amphipleura rutilans* (Trent.) Cleve; L = 24 μm.
8. *Mastogloia exigua* Lewis; L = 30 μm; a: focus down, b: focus up.
9. *Mastogloia exigua* Lewis; L = 35 μm; a: focus up, b: focus down.
10. *Gyrosigma eximium* (Thwaites) Boyer; L = 90 μm; a: entire valve, b: central and terminal nodules.
11. *Gyrosigma eximium* (Thwaites) Boyer; L = 86 μm.
12. *Gyrosigma exile* (Grunow) Reimer; L = 88 μm.
13. *Frustulia asymmetrica* (Cleve) Hustedt; L = 65 μm.
14. *Frustulia interposita* (Lewis) Cleve; L = 100 μm.

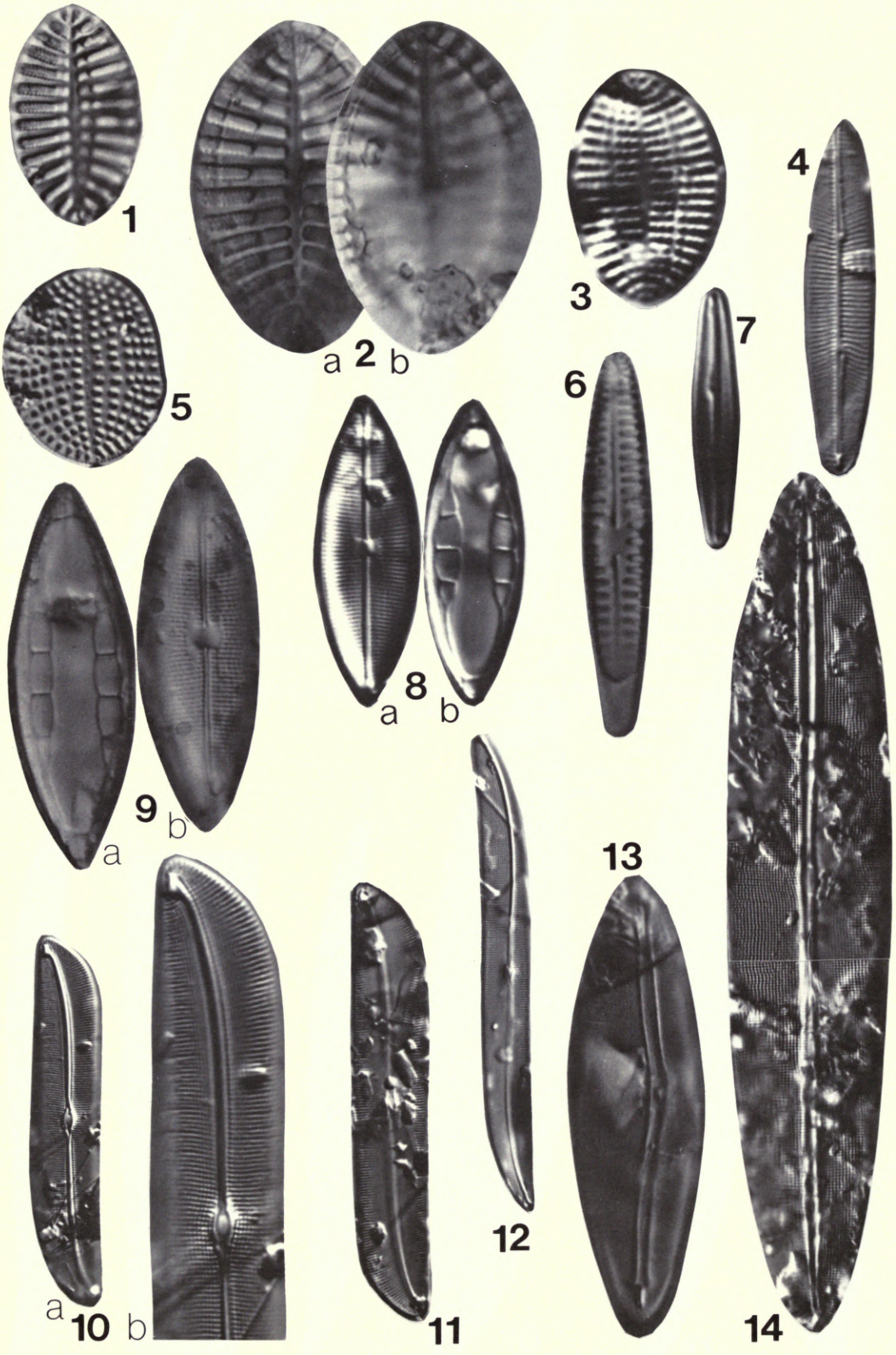

1
a 2 b
3
4
5
6
7
a 8 b
a 9 b
10 a b
11
12
13
14

Plate 20

FIGURE:

1. *Gyrosigma exile* (Grunow) Reimer; L = 80 μm.
2. *Gyrosigma fasciola* (Ehrenberg) Griffen and Henfrey; L = 112 μm.
3. *Gyrosigma acuminatum* (Kutzing) Rabenhorst; L = 84 μm.
4. *Gyrosigma acuminatum* (Kutzing) Rabenhorst; L = 84 μm.
5. *Gyrosigma balticum* (Ehrenberg) Rabenhorst; L = 250 μm; a: entire valve, b: central area.
6. *Pleurosigma diverse-striatum* Meist.; L = 108 μm.
7. *Pleurosigma angulatum* (Queckett) Smith?; ×1,250; polar nodule showing perpendicular striae.
8. *Pleurosigma* sp. 1; L = 240 μm; a: entire valve, b: central area.
9. *Pleurosigma* sp. 1; L = 256 μm.
10. *Pleurosigma* sp. 2; L = 220 μm.
11. *Pleurosigma normanii* Ralfs *in* Pritchard; L = 216 μm.
12. *Pleurosigma normanii* Ralfs *in* Pritchard; L = 190 μm.

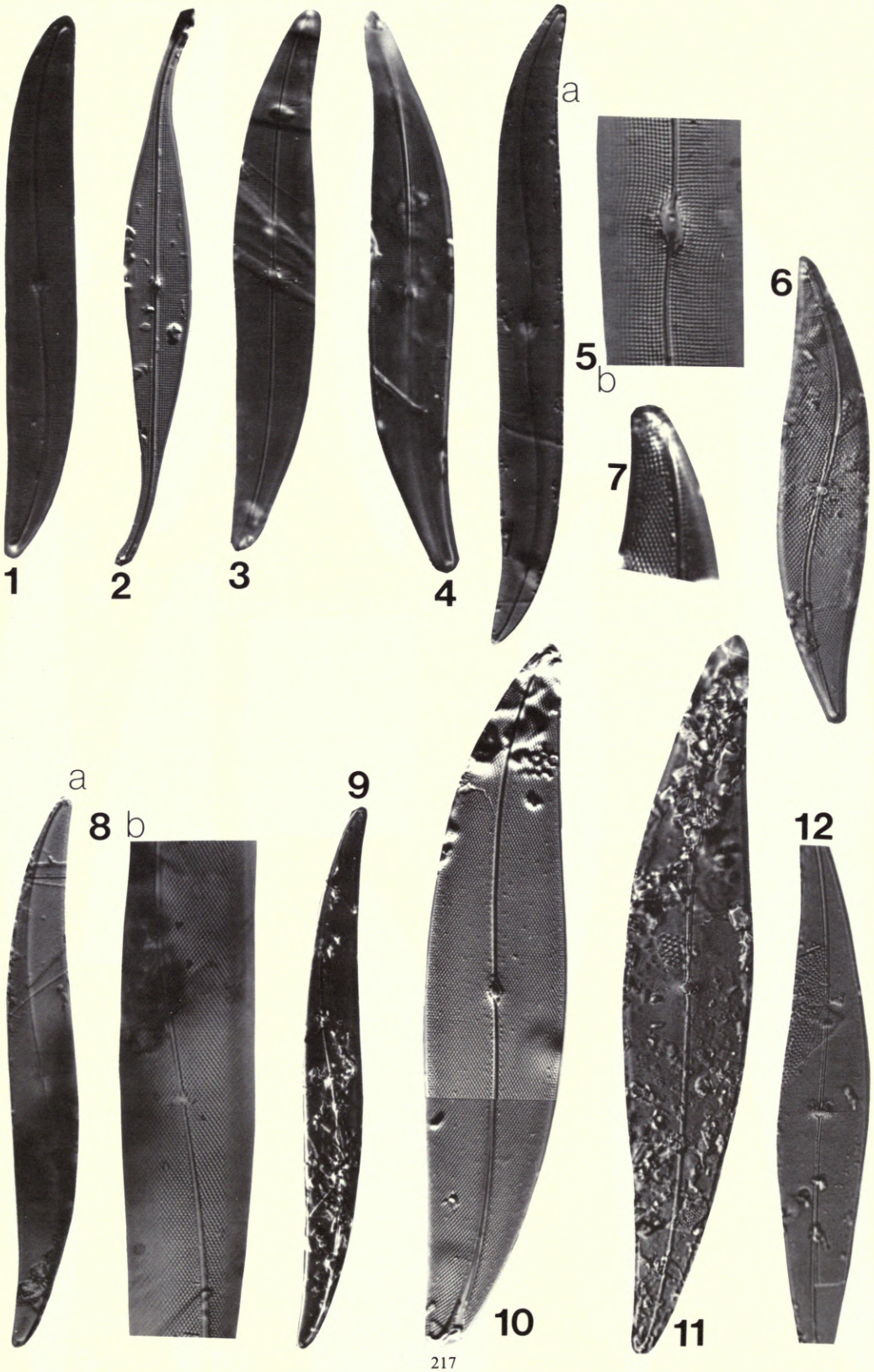

1
2
3
4
a
5
b
6
7
a
8
b
9
10
11
12

Plate 21

FIGURE:

1. *Pleurosigma strigosum* Smith; L = 232 μm.
2. *Pleurosigma strigosum* Smith; L = 201 μm.
3. *Pleurosigma strigosum* Smith; L = 160 μm; a: entire valve, b: central area and terminal nodule.
4. *Pleurosigma strigosum* Smith; L = 230 μm; a: entire valve, b: end, c: central area.
5. *Pleurosigma formosum* Smith; L = 525 μm.
6. *Pleurosigma australe* Grunow; L = 109 μm.
7. *Pleurosigma australe* Grunow; L = 102 μm.
8. *Pleurosigma angulatum* Smith?; L = 110 μm. (For half of valve.)
9. *Stauroneis obtusa* Lagerstedt; L = 32 μm.
10. *Stauroneis smithii* var. *incisa* Pantocsek; L = 30 μm.

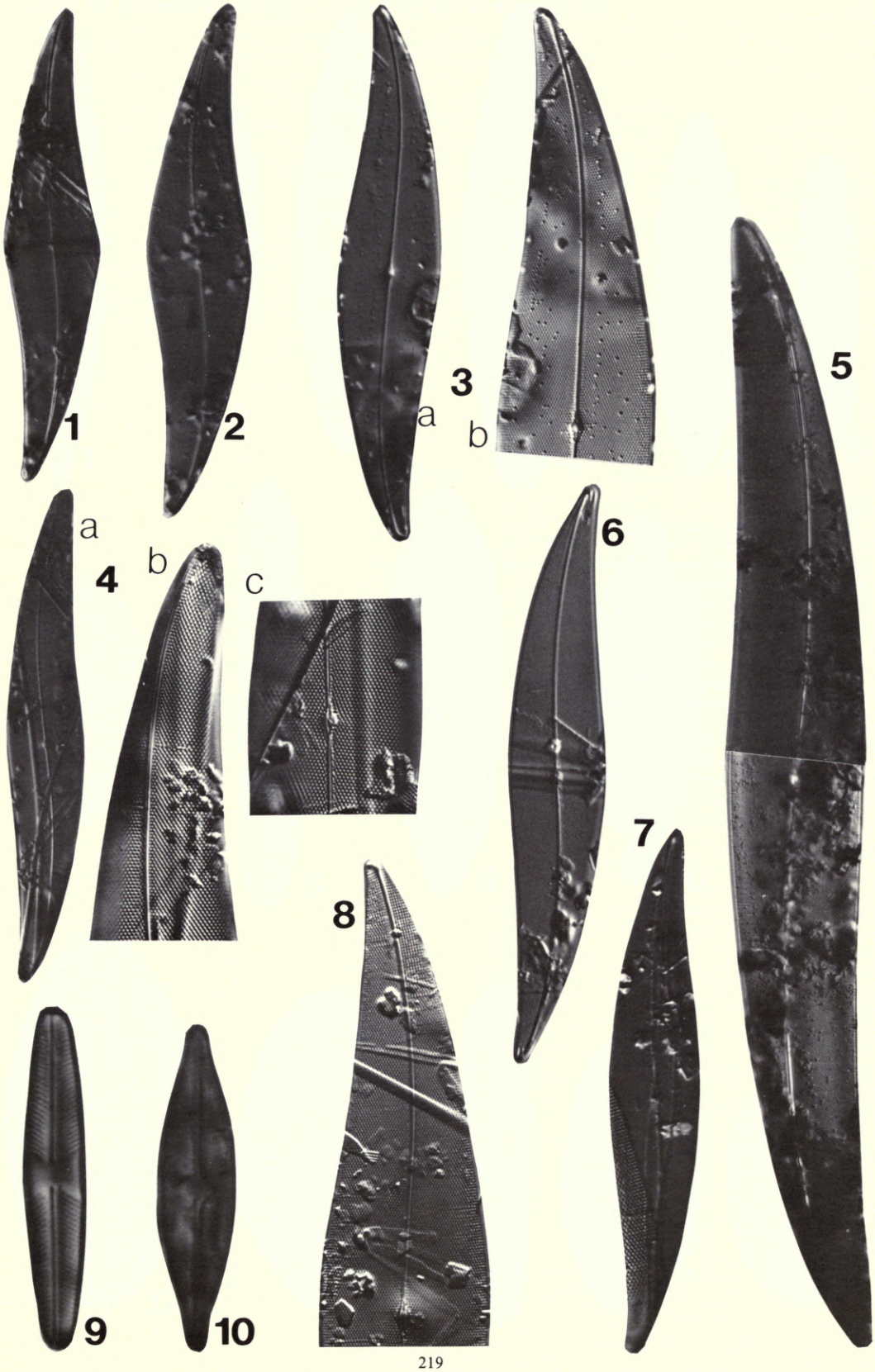

1
2
3
a
b
5
a
4
b
c
6
7
8
9
10

Plate 22

FIGURE:

1. *Stauroneis acuta* Smith; L = 80 μm.
2. *Stauroneis amphioxys* Gregory; L = 40 μm.
3. *Anomoeoneis sphaerophora* f. *costata* (Kutzing) Schmid; L = 75 μm.
4. *Caloneis westii* (Smith) Hendey; L = 88 μm.
5. *Caloneis westii* (Smith) Hendey; L = 65 μm.
6. *Caloneis bacillum* (Grunow) Cleve; L = 29 μm.
7. *Diploneis smithii* (Brébisson) Cleve; L = 38 μm.
8. *Caloneis alpestris* (Grunow) Cleve; L = 67 μm.
9. *Caloneis westii* (Smith) Hendey; L = 77 μm.
10. *Caloneis amphisbaena* (Bory) Cleve; L = 72 μm.
11. *Caloneis bacillum* (Grunow) Cleve; L = 39 μm.
12. *Diploneis smithii* (Brébisson) Cleve; L = 36 μm.
13. *Diploneis smithii* (Brébisson) Cleve; L = 29 μm.
14. *Caloneis ventricosa* (Ehrenberg) Meister; L = 61 μm.
15. *Diploneis oblongella* (Naeg. *in* Kutzing) Ross; L = 29 μm.
16. *Diploneis oblongella* (Naeg. *in* Kutzing) Ross; L = 25 μm.

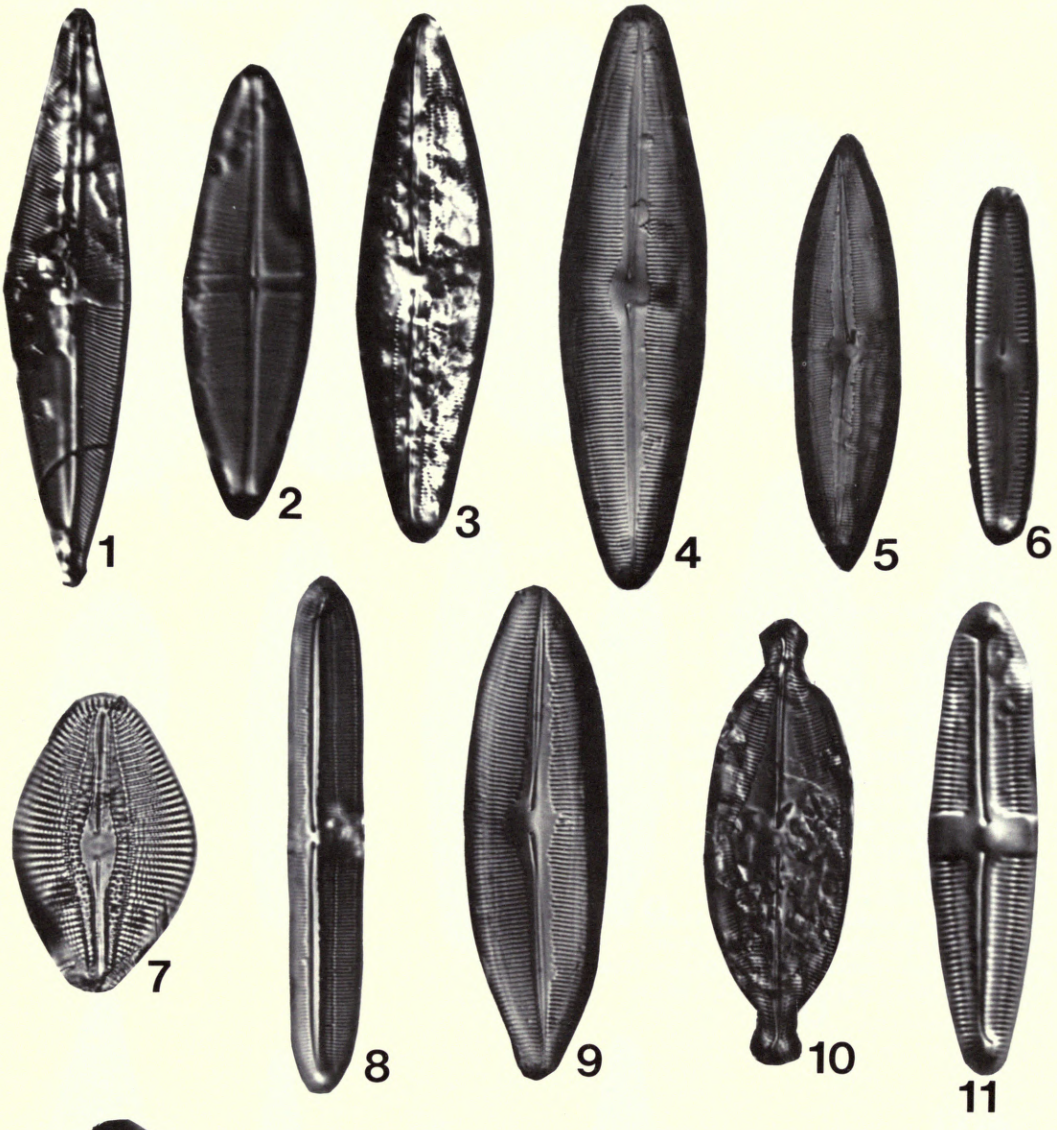

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

Plate 23

FIGURE:

1. *Diploneis interrupta* (Kutzing) Cleve; L = 40 μm.
2. *Diploneis interrupta* (Kutzing) Cleve; L = 60 μm.
3. *Diploneis bombus* Ehrenberg; L = 51 μm.
4. *Diploneis* sp. 6; L = 27 μm.
5. *Diploneis decipiens* Cleve-Euler; L = 16 μm.
6. *Diploneis papula* var. *constricta* Hustedt; L = 21 μm.
7. *Navicula circumtexta* Meister *in* Hustedt; L = 29 μm.
8. *Navicula circumtexta* Meister *in* Hustedt; L = 29 μm.
9. *Navicula cryptocephala* Kutzing; L = 24 μm.
10. *Navicula aurora* Sovereign; L = 64 μm.
11. *Navicula cuspidata* (Kutzing) Kutzing; L = 69 μm.
12. *Navicula cuspidata* (Kutzing) Kutzing; L = 88 μm.
13. *Navicula abunda* Hustedt; L = 71 μm.
14. *Navicula cryptocephala* Kutzing; L = 34 μm.
15. *Navicula cryptocephala* Kutzing; L = 34 μm.
16. *Navicula digito-radiata* (Gregory) Ralfs; L = 48 μm.
17. *Navicula distans* (Smith) Schmidt; L = 80 μm.

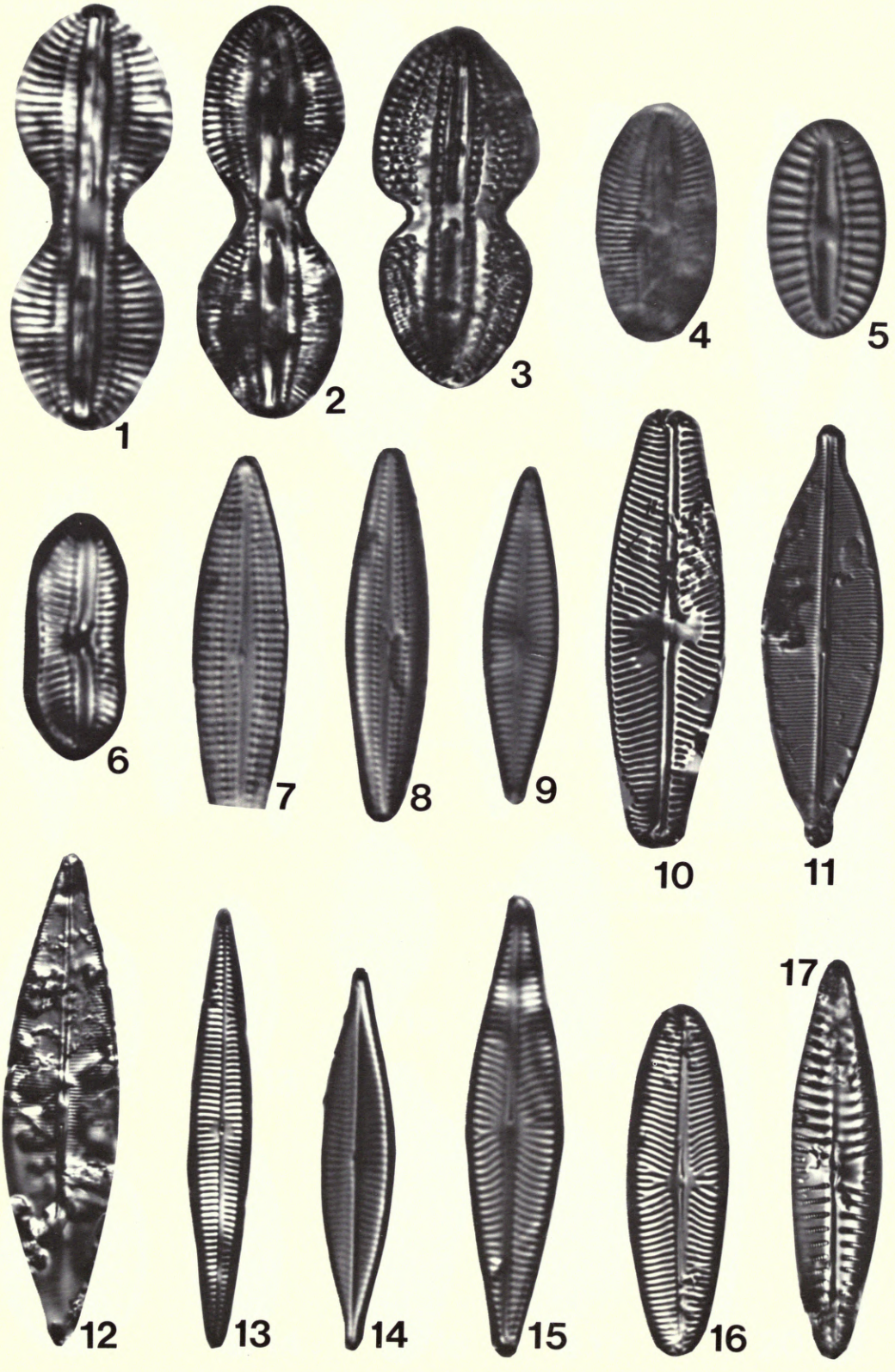

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

Plate 24

FIGURE:

1. *Navicula punctulata* Smith; L = 93 μm.
2. *Navicula granulata* Bailey; L = 60 μm.
3. *Navicula elginensis* (Gregory) Ralfs; L = 32 μm.
4. *Navicula gregaria* Donkin; L = 24 μm.
5. *Navicula gregaria* Donkin; L = 22 μm.
6. *Navicula salinarum* Grunow; L = 34 μm.
7. *Navicula salinarum* Grunow; L = 24 μm.
8. *Navicula salinarum* Grunow; L = 28 μm.
9. *Navicula gregaria* Donkin; L = 22 μm.
10. *Navicula gregaria* Donkin; L = 23 μm.
11. *Navicula gregaria* Donkin; L = 27 μm.
12. *Navicula hummii* Hustedt; L = 19 μm; a: focus up, b: focus down.
13. *Navicula mutica* Kutzing; L = 22 μm.
14. *Navicula mutica* Kutzing; L = 16 μm.
15. *Navicula pusilla* var. 1; L = 14 μm.
16. *Navicula pusilla* Smith; L = 38 μm.
17. *Navicula pusilla* var. 1; L = 25 μm.
18. *Navicula pygmeae* Kutzing; L = 24 μm.
19. *Navicula peregrina* (Ehrenberg) Kutzing; L = 113 μm.
20. *Navicula peregrina* (Ehrenberg) Kutzing; L = 120 μm.

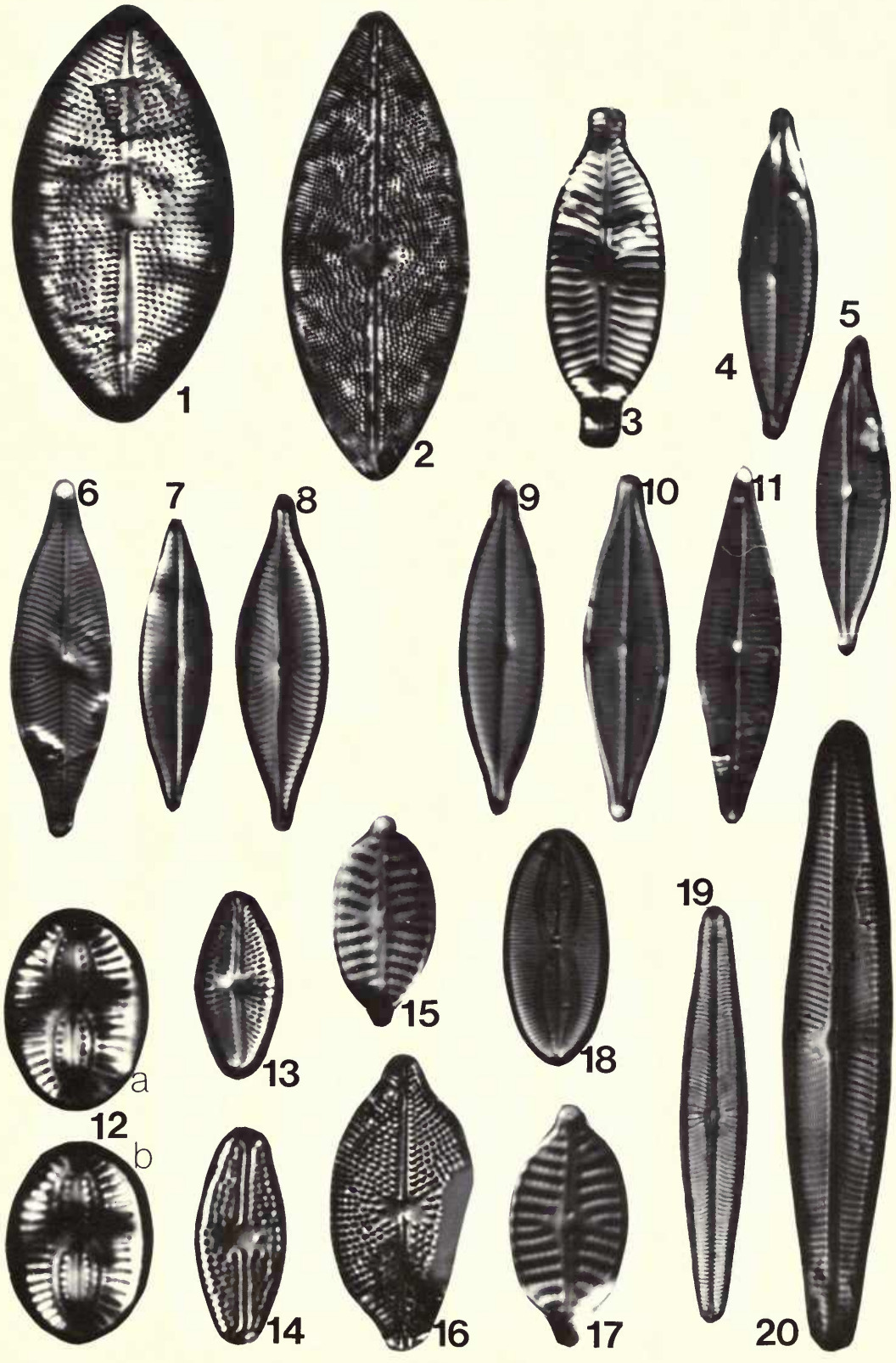

1
2
3
4
5
6
7
8
9
10
11
a
12
b
13
14
15
16
17
18
19
20

Plate 25

FIGURE:

1. *Navicula peregrina* (Ehrenberg) Kutzing; L = 55 μm.
2. *Navicula expansa* Haglestein; L = 83 μm; a: focus down, b: focus up.
3. *Navicula pygmeae* Kutzing; L = 32 μm.
4. *Navicula pygmeae* Kutzing; L = 24 μm.
5. *Navicula subforcipata* Hustedt; L = 16 μm.
6. *Navicula pseudolanceolata* Lange-Bertalot; L = 52 μm.
7. *Navicula auriculata* Hustedt; L = 10 μm.
8. *Achnanthes lanceolata* Brébisson; L = 17 μm.
9. *Achnanthes lanceolata* Brébisson; L = 20 μm.
10. *Navicula secreta* var. *apiculata* Patrick; L = 33 μm.
11. *Navicula scopulorum* Brébisson *in* Kutzing; L = 221 μm; a: entire valve, b: central area.
12. *Navicula reichardtii* var. *tschuktschorum* Cleve; L = 11 μm.
13. *Navicula spicula* (Hickie) Cleve; L = 56 μm.
14. *Pinnularia borealis* Ehrenberg; L = 34 μm; a: entire valve, b: central and polar nodules.
15. *Navicula tripunctata* (Muller) Bory; L = 42 μm.
16. *Navicula tripunctata* (Muller) Bory; L = 40 μm.
17. *Navicula tripunctata* (Muller) Bory; L = 30 μm.
18. *Navicula tripunctata* (Muller) Bory; L = 26 μm.

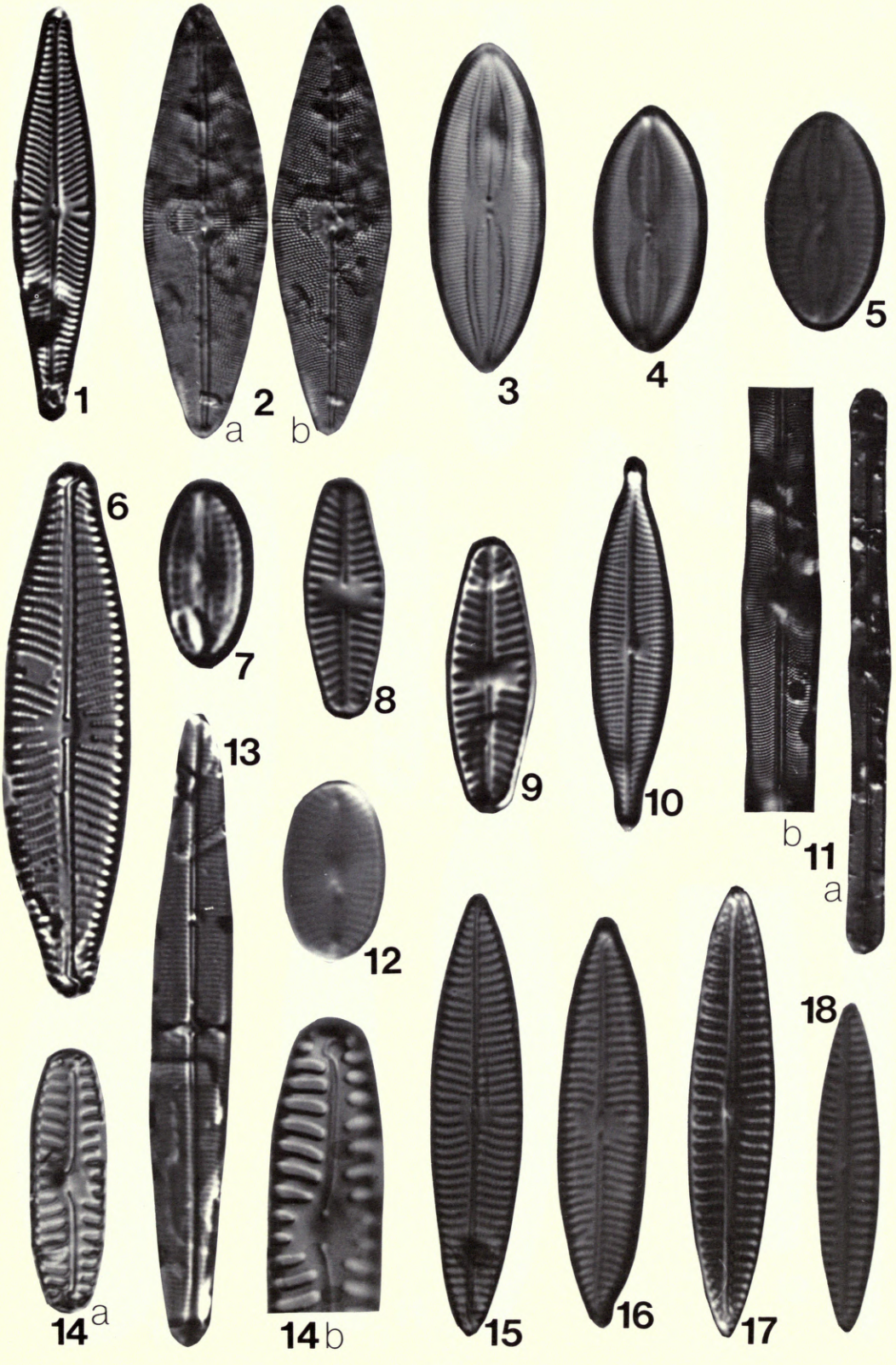

1
2
a
b
3
4
5
6
7
8
9
10
11
a
b
12
13
14
a
14
b
15
16
17
18

Plate 26

FIGURE:

1. *Pinnularia borealis* Ehrenberg; L = 56 μm; a: focus up, b: focus down.
2. *Pinnularia borealis* var. *brevicostata* Hustedt; L = 57 μm.
3. *Pinnularia subcapitata* var. *paucistriata* (Grunow) Cleve; L = 40 μm.
4. *Pinnularia gibba* Ehrenberg; L = 48 μm.
5. *Pinnularia gibba* Ehrenberg; L = 59 μm.
6. *Pinnularia acuminata* Smith; L = 43 μm.
7. *Pinnularia abaujensis* var. *rostrata* (Patr.) Patrick; L = 48 μm.
8. *Pinnularia microstauron* var. *biundulata* O. Müller; L = 59 μm.
9. *Scoliopleura tumida* (Brébisson *in* Kutzing) Rabenhorst; L = 89 μm.
10. *Entomoneis paludosa* (Smith) Reimer; L = 40 μm.
11. *Entomoneis* sp. 1; L = 109 μm; a: focus down, b: focus up.
12. *Scoliotropis latestriata* (Brébisson *in* Kutzing) Cleve; L = 260 μm; a: entire valve, b: central area.

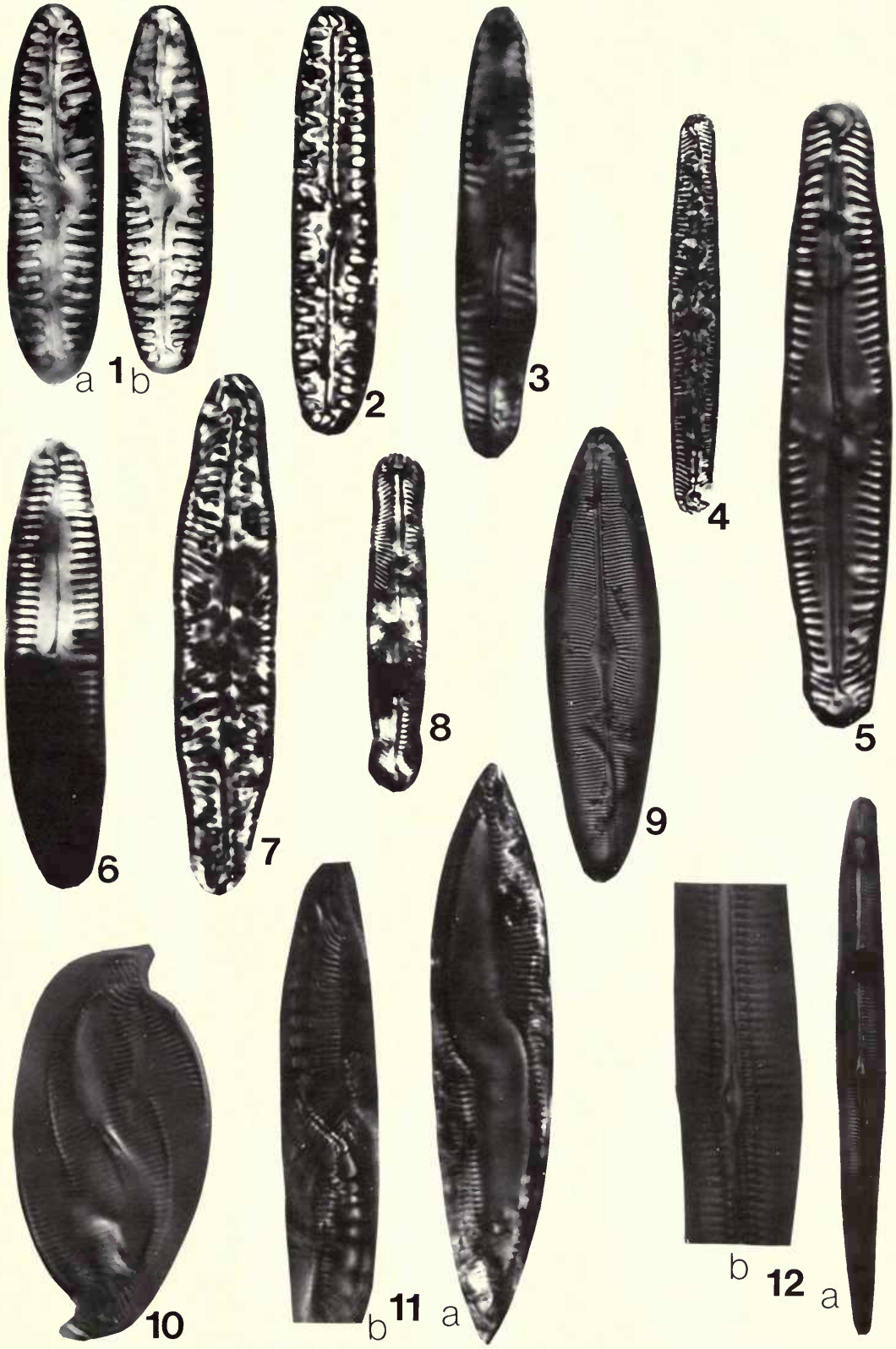

a 1 b
2
3
4
5
6
7
8
9
10
b 11 a
b 12 a

Plate 27

FIGURE:

1. *Entomoneis alata* (Ehrenberg) Ehrenberg; L = 88 μm.
2. *Plagiotropis vitrea* (Smith) comb. nov.; L = 82 μm.
3. *Plagiotropis vitrea* (Smith) comb. nov.; L = 96 μm.
4. *Amphora ovalis* (Kutzing) Kutzing; L = 23 μm.
5. *Amphora granulata* Gregory; L = 24 μm.
6. *Amphora* sp. 1; L = 43 μm.
7. *Amphora granulata* Gregory; L = 74 μm.
8. *Amphora granulata* Gregory; L = 40 μm.
9. *Amphora ventricosa* (Gregory) Hendey; L = 43 μm.
10. *Amphora sublaevis* Hustedt; L = 51 μm.
11. *Cymbella prostrata* (Berk.) Cleve; L = 56 μm.
12. *Cymbella triangulum* (Ehrenberg) Cleve; L = 50 μm.
13. *Cymbella sinuata* Gregory; L = 15 μm.
14. *Cymbella minuta* Hilse *in* Rabenhorst; L = 24 μm.
15. *Cymbella prostrata* var. *auerswaldii* (Rabhorst) Reimer *in* Patrick and Reimer; L = 28 μm.

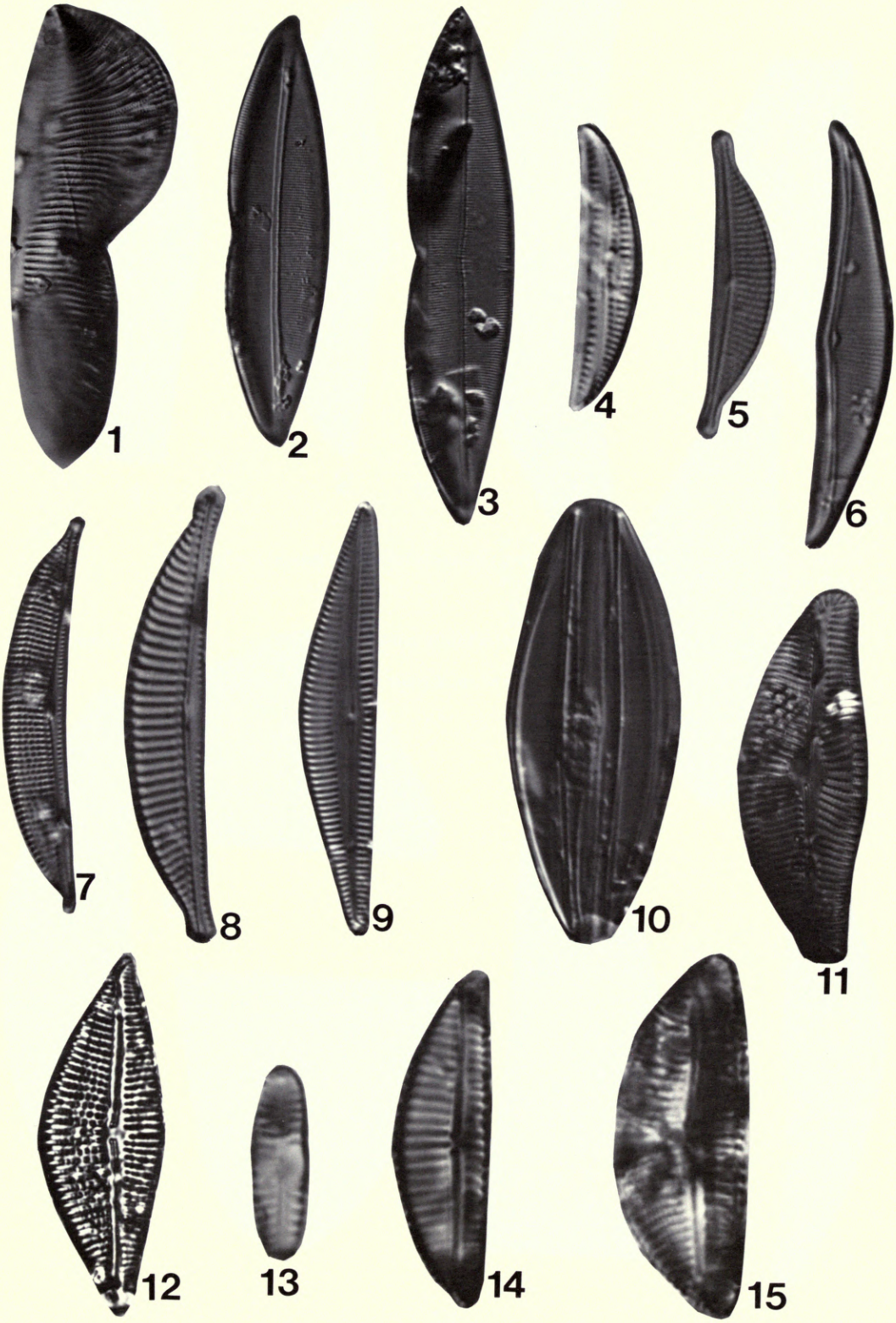

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

Plate 28

FIGURE:

1. *Cymbella triangulum* (Ehrenberg) Cleve; L = 50 μm.
2. *Cymbella muellerii* var. *ventricosa* (Temp. and Perg.) Reimer *in* Patrick and Reimer; L = 74 μm.
3. *Cymbella mexicana* (Ehrenberg) Cleve; L = 112 μm.
4. *Cymbella mexicana* (Ehrenberg) Cleve; L = 85 μm.
5. *Cymbella mexicana* (Ehrenberg) Cleve; L = 90 μm.
6. *Cymbella mexicana* var. *janischii* (Schmidt) Reimer *in* Patrick and Reimer; L = 200 μm; a: entire valve, b: central area, c: polar nodule.
7. *Cymbella cistula* (Ehrenberg) Kirchn. *in* Cohn; L = 88 μm; a: entire valve, b: central and polar nodules.

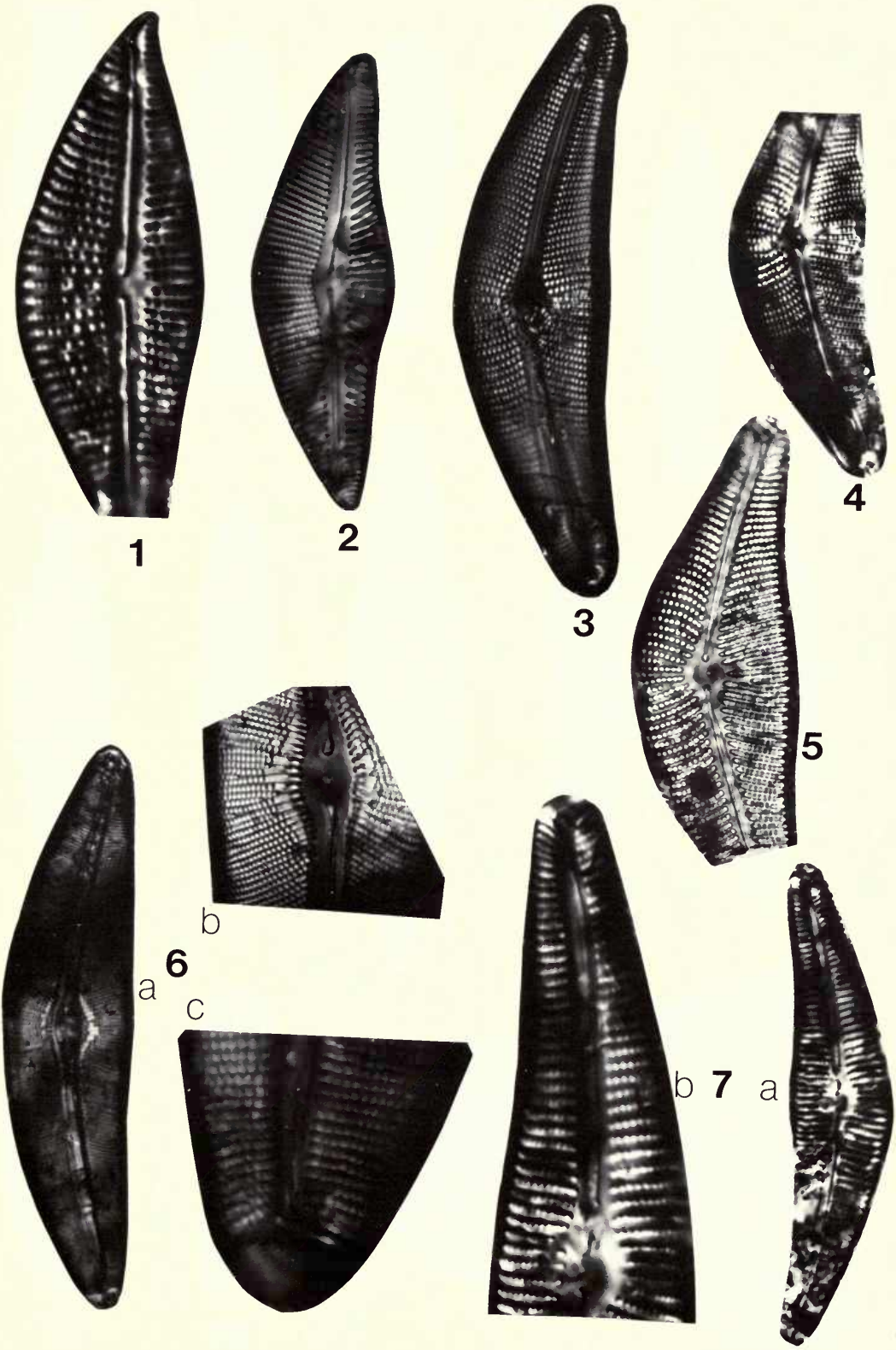

1
2
3
4
5
6
a
b
c
7
a
b

Plate 29

FIGURE:

1. *Gomphonema ventricosum* Gregory; L = 44 μm.
2. *Gomphonema ventricosum* Gregory; L = 40 μm.
3. *Gomphonema grovei* M. Schmidt; L = 26 μm.
4. *Gomphonema gracile* (Ehrenberg) emend. Van Heurck; L = 24 μm.
5. *Gomphonema angustatum* var. *sarcophagus* (Greg.) Grun.; L = 26 μm.
6. *Gomphonema angustatum* var. *sarcophagus* (Greg.) Grun.; L = 36 μm.
7. *Gomphonema parvulum* (Kutzing) Kutzing; L = 23 μm.
8. *Gomphonema rhombicum* Fricke; L = 29 μm.
9. *Gomphonema septum* Moghadam; L = 48 μm.
10. *Gomphonema affine* Kutzing; L = 39 μm.
11. *Gomphoneis eriense* (Ehrenberg) Cleve; L = 80 μm.
12. *Gomphoneis herculeana* (Grunow) Skvortzow and Meyer; L = 32 μm.
13. *Trachyneis aspera* (Ehrenberg) Cleve; L = 156 μm.
14. *Auricula complexa* Gregory; L = 35 μm.

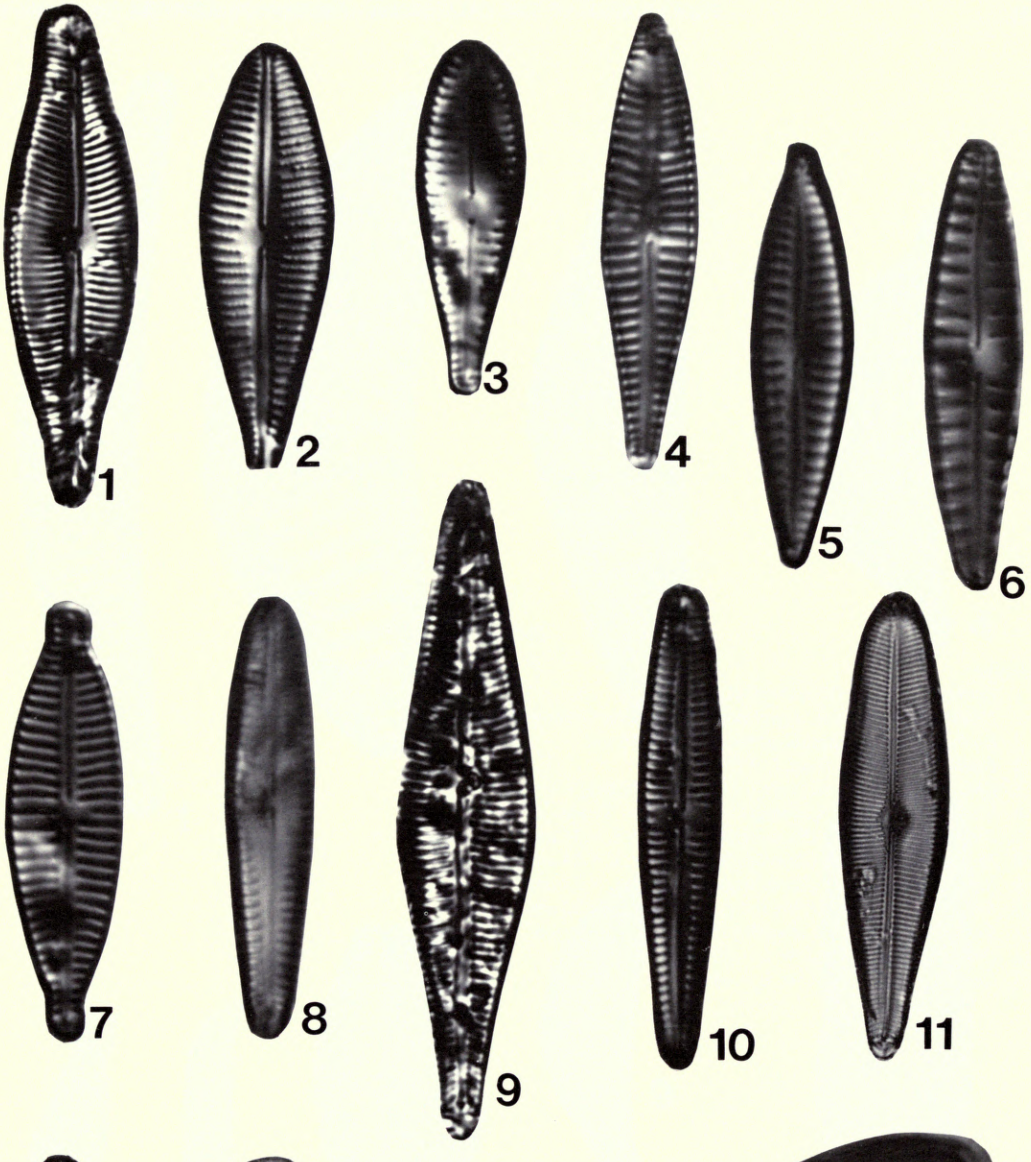

1
2
3
4
5
6
7
8
9
10
11
12
13
a
14
b

Plate 30

FIGURE:

1. *Epithemia turgida* (Ehrenberg) Kutzing; L = 76 μm.
2. *Epithemia turgida* var. *westermanii* (Ehrenberg) Grunow; L = 52 μm.
3. *Epithemia argus* (Ehrenberg) Kuzting; L = 56 μm.
4. *Epithemia sorex* Kutzing; L = 37 μm.
5. *Epithemia adnata* var. *porcellus* (Kutzing) Patrick; L = 61 μm.
6. *Rhopalodia gibba* (Ehrenberg) O. Müller; L = 71 μm.
7. *Rhopalodia gibberula* (Ehrenberg) O. Müller; L = 34 μm; girdle view.
8. *Rhopalodia gibberula* (Ehrenberg) O. Müller; L = 24 μm.
9. *Rhopalodia gibberula* (Ehrenberg) O. Müller; L = 23 μm.
10. *Rhopalodia gibberula* (Ehrenberg) O. Müller; L = 22 μm.
11. *Rhopalodia operculata* (Agardh) Hakansson; L = 24 μm.
12. *Denticula subtilis* Grunow; L = 30 μm.
13. *Denticula subtilis* Grunow; L = 18 μm.

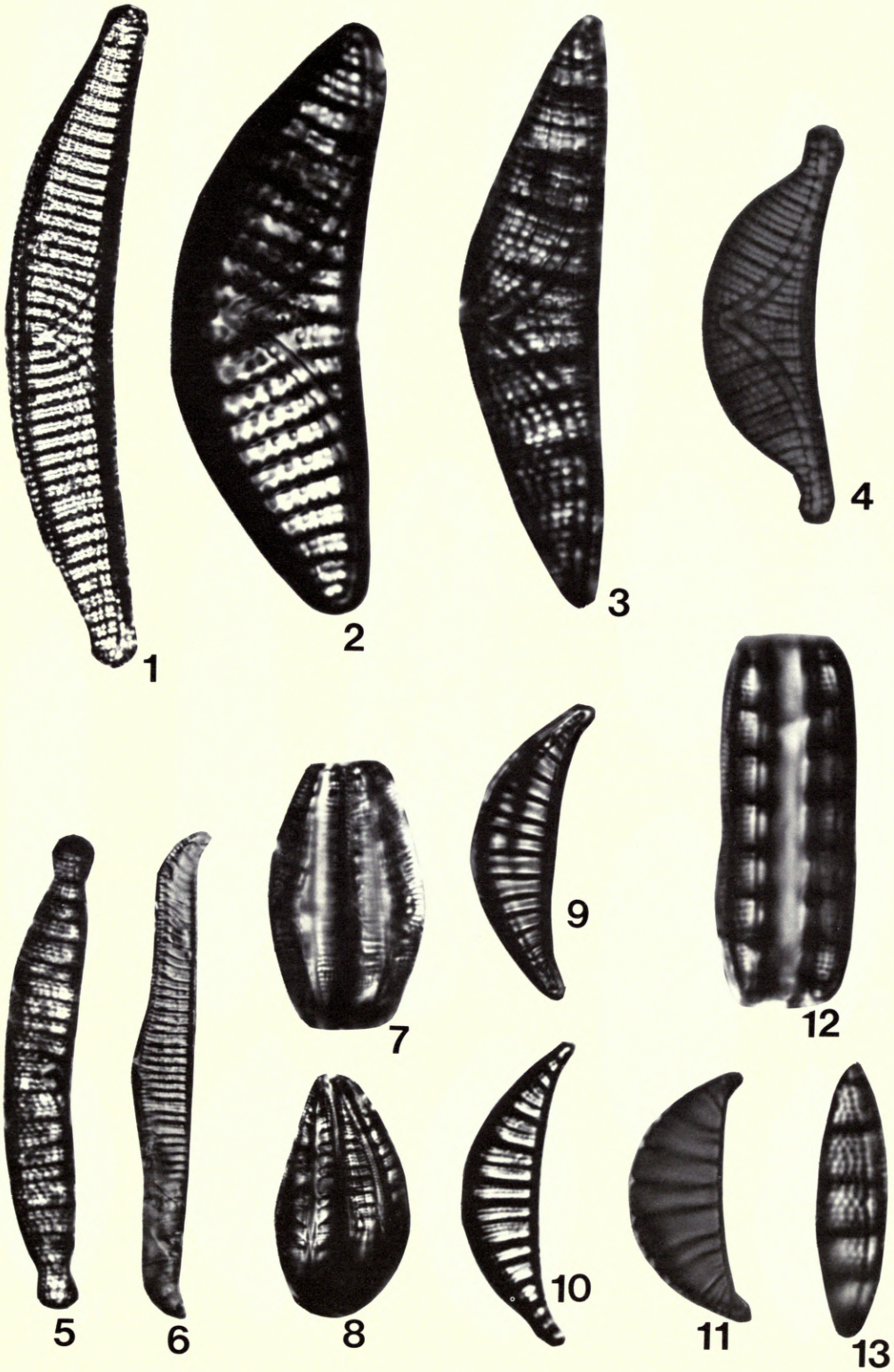

1
2
3
4
5
6
7
8
9
10
11
12
13

Plate 31

FIGURE:

1. *Pseudoeunotia doliolus* (Wallich) Grunow *in* Van Heurck; L = 52 μm.
2. *Bacillaria paxillifer* (O. F. Müller) Hendey; L = 75 μm.
3. *Hantzschia amphioxys* (Ehrenberg) Grunow; L = 72 μm.
4. *Nitzschia tryblionella* Hantzsch; L = 56 μm; a: focus down, b: focus up.
5. *Nitzschia tryblionella* Hantzsch; L = 45 μm.
6. *Nitzschia tryblionella* Hantzsch; L = 72 μm.
7. *Nitzschia acuminata* (Smith) Grunow; L = 30 μm.
8. *Nitzschia acuminata* (Smith) Grunow; L = 44 μm.
9. *Nitzschia circumsuta* (Bailey) Grunow; L = 184 μm.
10. *Nitzschia levidensis* (Smith) Van Heurck; L = 56 μm.
11. *Nitzschia punctata* (Smith) Grunow; L = 50 μm.
12. *Nitzschia punctata* (Smith) Grunow; L = 24 μm.
13. *Nitzschia punctata* (Smith) Grunow; L = 37 μm.
14. *Nitzschia punctata* (Smith) Grunow; L = 21 μm.

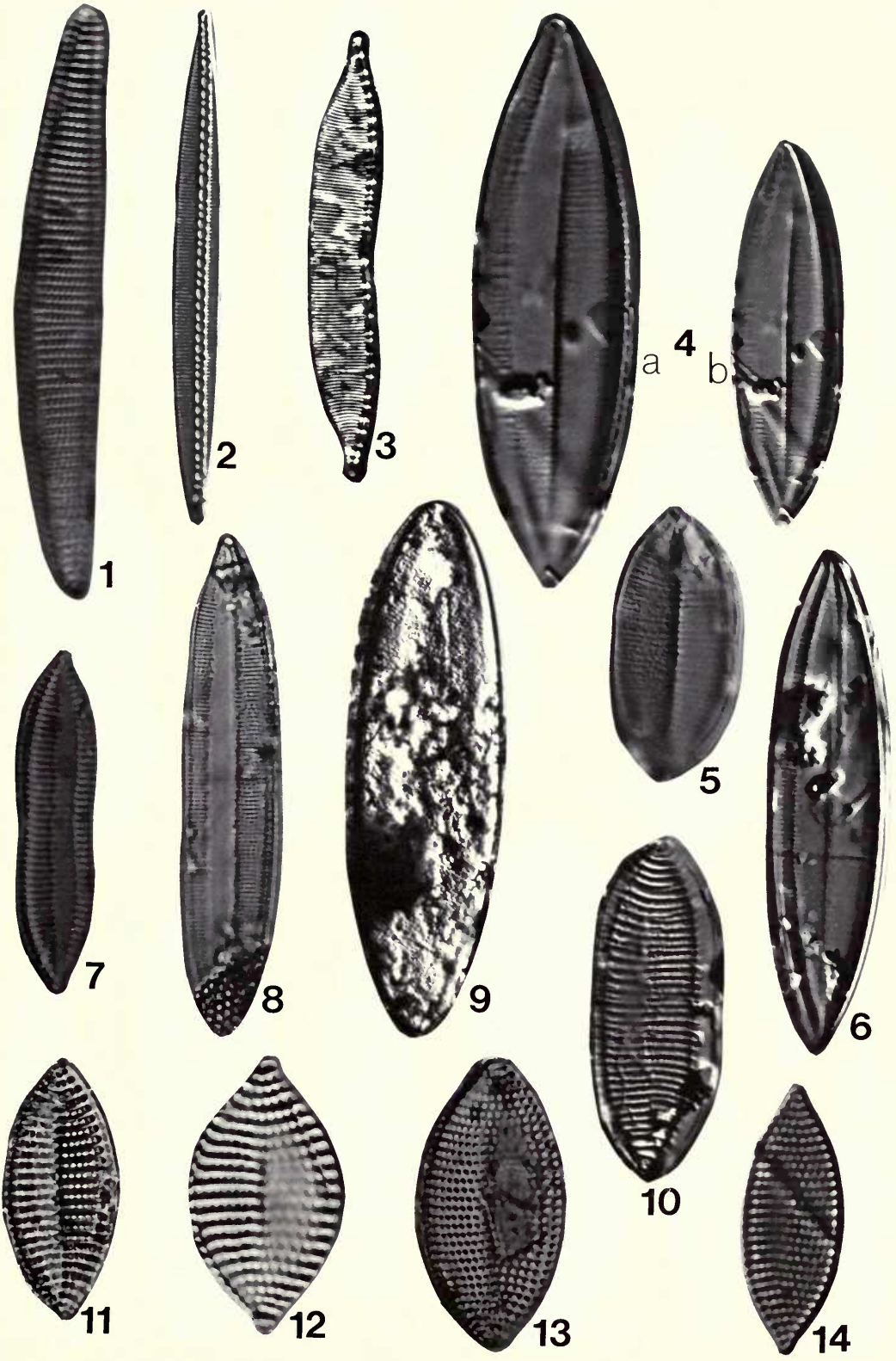

1
2
3
4
a
b
5
6
7
8
9
10
11
12
13
14

Plate 32

FIGURE:

1. *Nitzschia navicularis* (Brébisson) Grunow; L = 72 μm; a: focus up, b: focus down.
2. *Nitzschia granulata* Grunow; L = 48 μm; a: bright field, b: dark field
3. *Nitzschia granulata* var. 1; L = 39 μm.
4. *Nitzschia granulata* var. 1; L = 50 μm.
5. *Nitzschia granulata* var. 1; L = 42 μm; a: focus down, b: focus up.
6. *Nitzschia punctata* var. *coarcta* (Grunow) Hustedt; L = 33 μm.
7. *Nitzschia panduriformis* Gregory; L = 30 μm.
8. *Nitzschia* sp. 1; L = 26 μm.
9. *Nitzschia pseudohybrida* Hustedt; L = 81 μm.
10. *Nitzschia pseudohybrida* Hustedt; L = 59 μm.
11. *Nitzschia dissipata* (Kutzing) Grunow; L = 32 μm.
12. *Nitzschia plana* Smith; L = 99 μm.
13. *Nitzschia pusilla* (Kutzing) Grunow; L = 17 μm.
14. *Nitzschia pusilla* (Kutzing) Grunow; L = 27 μm.
15. *Nitzschia pusilla* (Kutzing) Grunow; L = 16 μm.

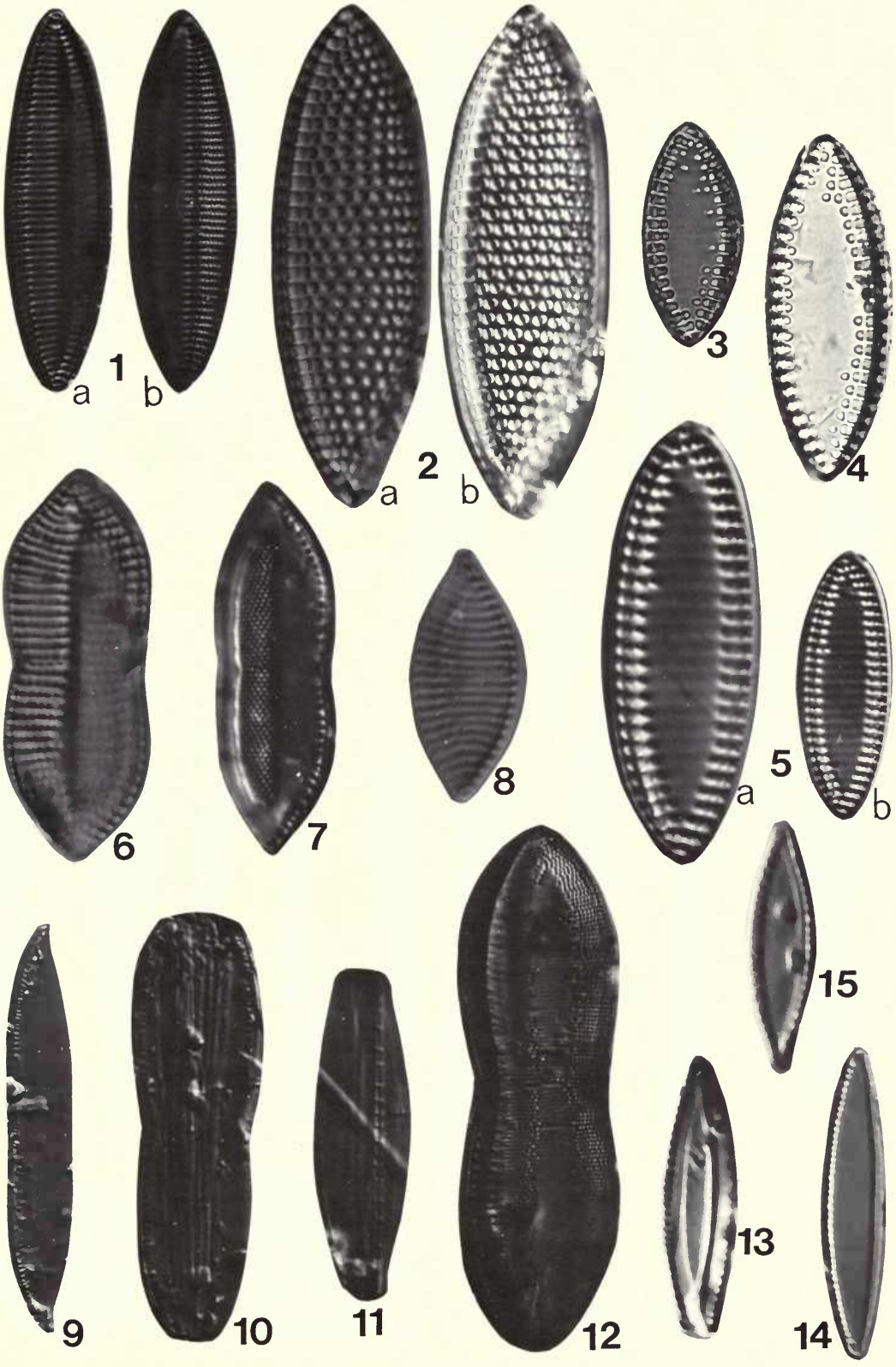

a
1
b
a
2
b
3
4
6
7
8
a
5
b
15
13
9
10
11
12
14

Plate 33

FIGURE:

1. *Nitzschia frustulum* (Kutzing) Grunow; L = 33 μm.
2. *Nitzschia gandersheimiensis* Krasske; L = 78 μm.
3. *Nitzschia gandersheimiensis* Krasske; L = 31 μm.
4. *Nitzschia gandersheimiensis* Krasske; L = 32 μm.
5. *Nitzschia vitrea* Norman; L = 68 μm.
6. *Nitzschia obtusa* var. *scalpeliformis* Grunow; L = 125 μm.
7. *Nitzschia sigmaformis* Hustedt; L = 120 μm.
8. *Nitzschia sigmaformis* Hustedt; L = 136 μm.
9. *Nitzschia longa* Grunow; L = 160 μm.
10. *Nitzschia angularis* Smith; L = 120 μm.
11. *Nitzschia closterium* (Ehrenberg) Smith; L = 120 μm.
12. *Campylodiscus ralfsii* Smith; D = 19 μm.
13. *Nitzschia hummii* Hustedt; L = 119 μm.
14. *Nitzschia fasciculata* Grunow; L = 48 μm.
15. *Nitzschia fasciculata* Grunow; L = 55 μm.
16. *Nitzschia sigma* (Kutzing) Smith; L = 120 μm.
17. *Nitzschia sigma* (Kutzing) Smith; L = 97 μm.
18. *Nitzschia sigma* (Kutzing) Smith; L = 176 μm.
19. *Campylodiscus incertus* A. Schmidt; D = 32 μm.

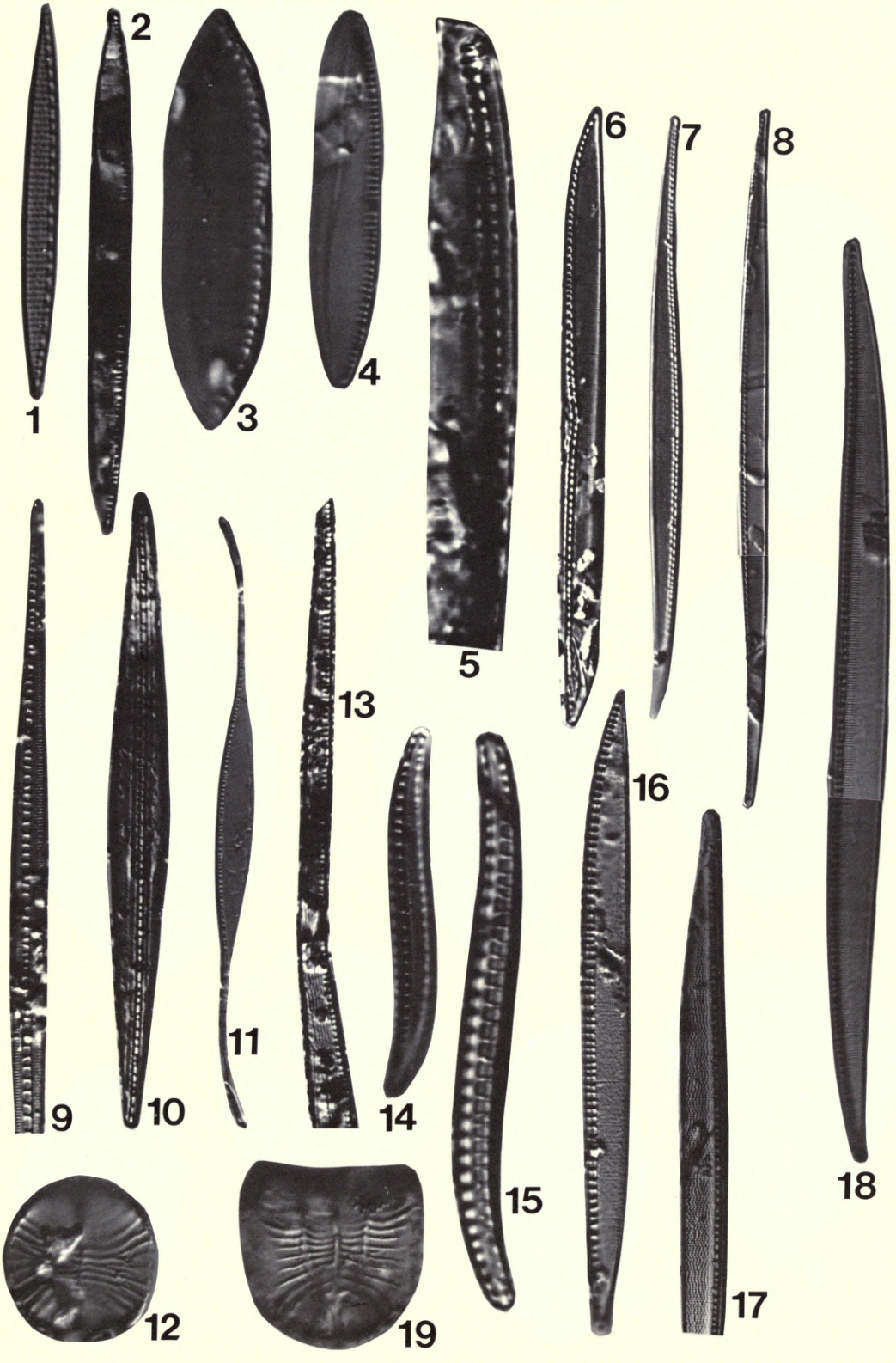

1
2
3
4
5
6
7
8
9
10
11
13
14
15
16
17
18
12
19

Plate 34

FIGURE:

1. *Surirella striatula* Turpin; L = 107 μm; a: focus down, b: focus up.
2. *Surirella ovata* Kutzing; L = 54 μm; a: dark field, b: bright field.
3. *Surirella fastuosa* (Ehrenberg) Kutzing; L = 91 μm.
4. *Surirella torquata* Pantocsek; L = 83 μm.
5. *Surirella fastuosa* (Ehrenberg) Kutzing; L = 85 μm.
6. *Surirella crumena* Brébisson *in* Kutzing; L = 47 μm.
7. *Surirella crumena* Brébisson *in* Kutzing; L = 56 μm.
8. *Surirella gemma* (Ehrenberg) Kutzing; L = 57 μm.
9. *Surirella peisonis* Pantocsek; L = 57 μm.

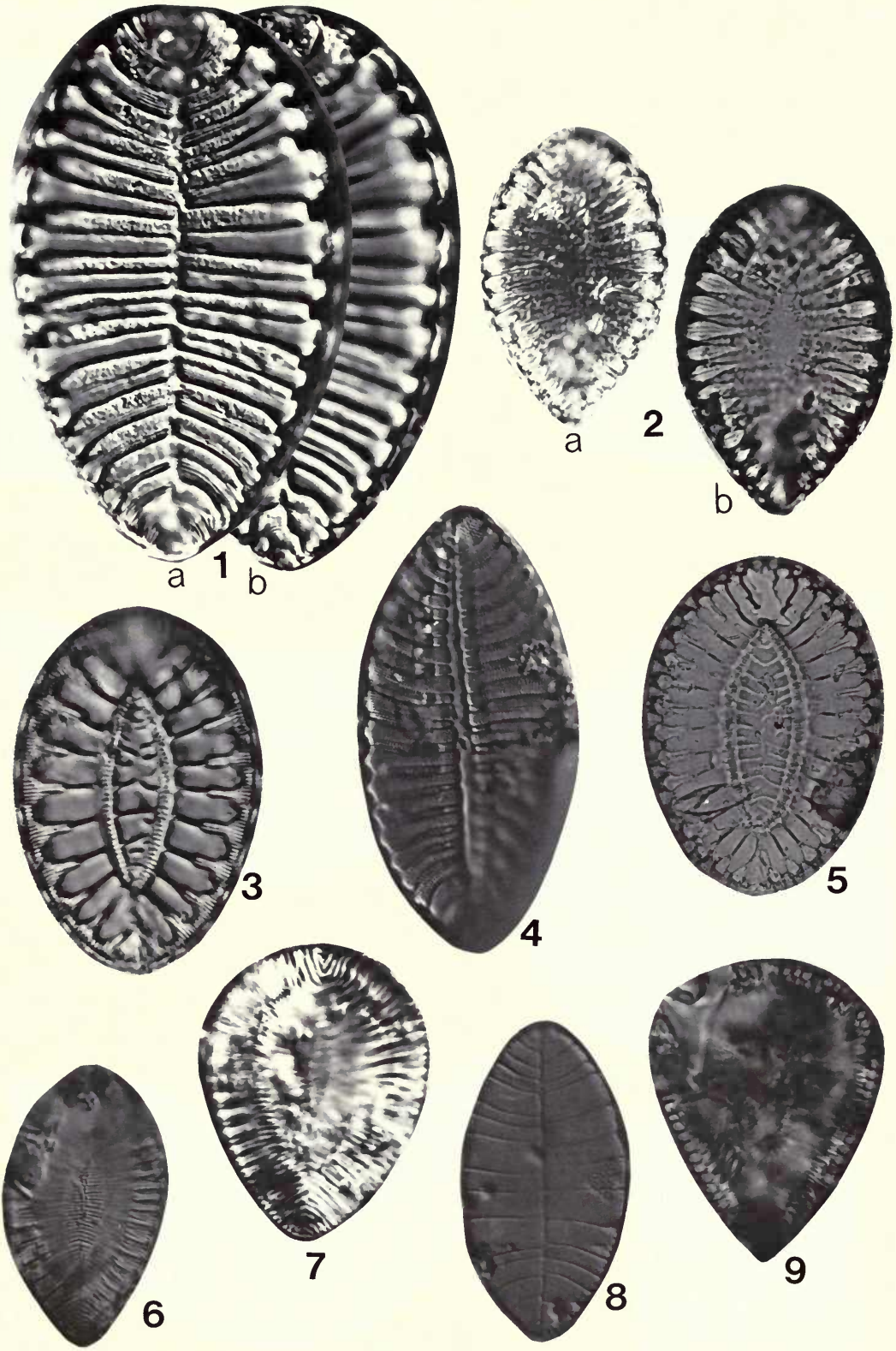
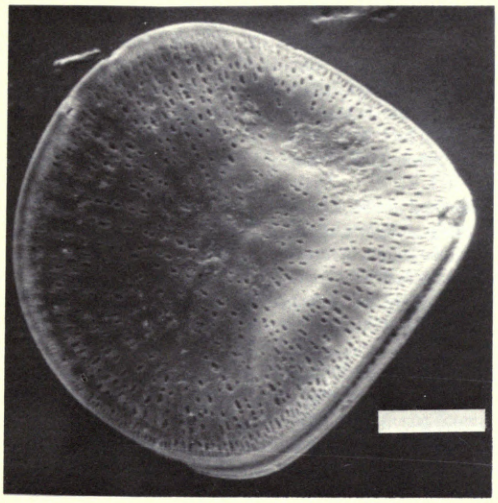
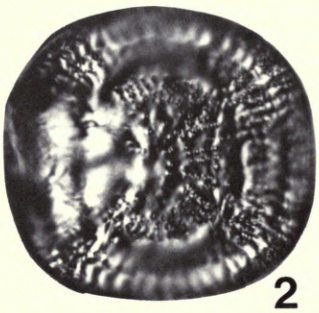

a
1
b
a
2
b
3
4
5
6
7
8
9

Plate 35

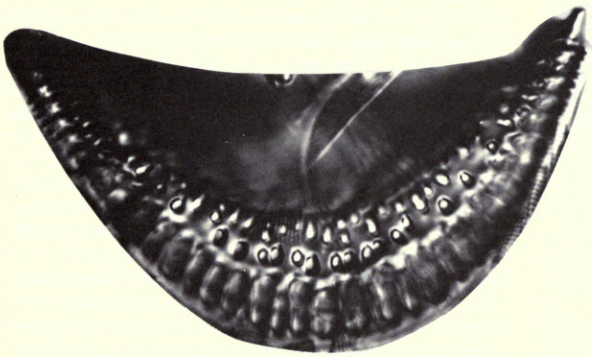
FIGURE:
1. *Campylodiscus echeneis* Ehrenberg; scale bar is 40 μm.
2. *Campylodiscus clypeus* Ehrenberg; D = 108 μm.
3. *Campylodiscus echeneis* Ehrenberg; L = 83 μm; a: focus down, b: focus up.
4. *Coscinodiscus marginatus* Ehrenberg; D = 83 μm; a: entire valve, b: areolae magnified.



1

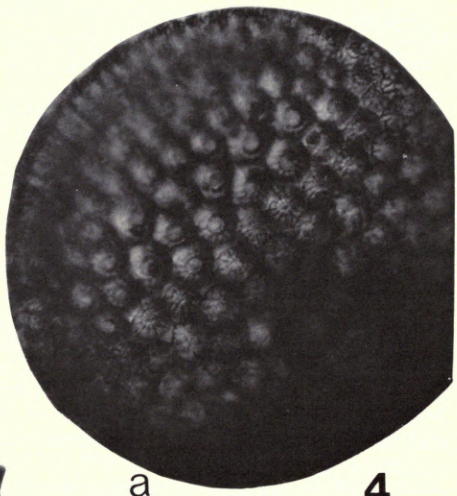


2



a

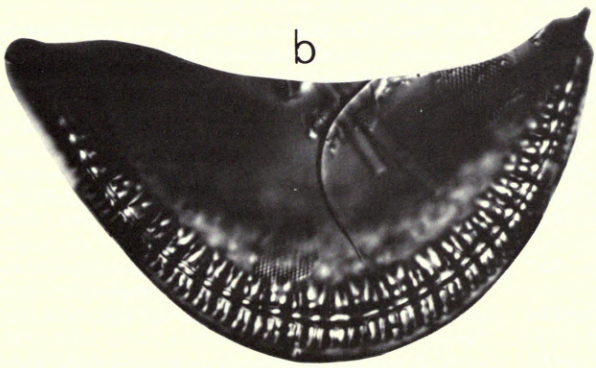
3



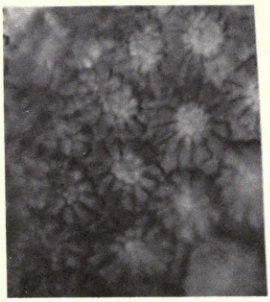
a

4

b



b



Literature Cited

Agardh, C. A. 1824. Systema Algarum. Lundae.

———. 1830. Conspectus Criticus Diatomacearum. Part 1, pp. 1–16. Lundae.

———. 1832. Conspectus Criticus Diatomacearum. Part 4, pp. 48–66. Lundae.

Amspoker, M. C. and C. D. McIntire. 1978. Distribution of intertidal diatoms associated with sediments in Yaquina Estuary, Oregon. J. Phycol. 14:382–395.

Arthur, J. F. and M. D. Ball. 1979. Factors influencing the entrapment of suspended material in the San Francisco Bay–Delta Estuary. Pp. 143–174 *in* San Francisco Bay: the urbanized estuary. T. J. Conomos, ed. Pacific Division, American Association for the Advancement of Science, San Francisco, California.

Atwater, B. F. 1979. Ancient processes at the site of southern San Francisco Bay: movement of the crust and changes in sea-level. Pp. 31–46 *in* San Francisco Bay: the urbanized estuary. T. J. Conomos, ed. Pacific Division, American Association for the Advancement of Science, San Francisco, California.

———. 1980. Attempts to correlate late Quaternary climatic records between San Francisco Bay, the Sacramento–San Joaquin Delta, and the Mokelumne River, California. Ph.D. Dissertation (unpubl.), Univ. of Delaware, 214 pp.

Atwater, B. F., C. W. Hedel, and E. J. Helly. 1977. Late Quaternary depositional history, Holocene sea-level changes, and vertical crustal movement, southern San Francisco Bay, California. U.S. Geological Survey Professional Paper 1014.

Bailey, J. W. 1849. Some remarks on the *Navicula Spencerii* and on a still more difficult test object. Am. J. Science ser. 2, 7:265–270.

———. 1853. Notes on new species and localities of microscopical organisms. Smithsonian Contributions to Knowledge 7(3):16.

———. 1861. Notes on new species of microscopical organisms chiefly from the Para River, South America. Boston J. Nat. Hist. 7:329–352.

Ball, M. D. and J. F. Arthur 1979. Planktonic chlorophyll dynamics in the Northern San Francisco bay and delta. Pp. 265–286 *in* San Francisco Bay: the urbanized estuary. T. J. Conomos, ed. Pacific Division, American Association for the Advancement of Science, San Francisco, California.

Barron, J. A. 1975. Late Miocene–Early Pliocene diatoms from southern California. Palaeontographica Abt. B 151:97–170.

Bory de Saint Vincent, J. 1822. Dictionnaire Classique d'Histoire Naturelle 1:79, Paris.

———. 1824. Pp. 562–563 *in* Encyclopedia Methodique Historie Naturelle des Zoophytes ou Animaux Rayonnes Vol. 2. Agasse, Paris.

Boyer, C. S. 1927. Synopsis of North American Diatomaceae, Parts 1 and 2. Proc. Acad. Nat. Sci. Phila., vol. 79, supplement, part 2, pp. 229–583.

Brébisson, A. 1838. Considerations sur les Diatomées et essai d'une classification des genres et des espeèes appartenant a cette famille. Bree l'Aine Imprimeur-Libraire Glaise, 22 pp.

Brightwell, T. 1858. Remarks on the genus "Rhizosolenia" of Ehrenberg. Q. J. Micros. Sci. 6:93–95.

———. 1859. On some of the rarer or undescribed species of Diatomacea, Part 1. Q. J. Micros. Sci. 7:179–181.

———. 1860. On some of the rarer or undescribed species of Diatomaceae, Part II. Q. J. Micros. Sci. 8:93–96.

Brooks, M. 1975. Studies on the genus *Coscinodiscus*. Bot. Mar. 18:1–39.

Brown, N. E. 1920. Some new and old antarctic diatoms. English Mechanic 3(III):232–233.

Brun, J. 1981. Diatomées espèces nouvelles marines, fossiles ou pelagiques. Memoires de la Societe de Physique et d'Histoire Naturelle de Geneve 31(1):1–47.

Carter, J. R. 1970. Diatoms from Andorra. Nova Hedwigia, Beihefte 31:605–632.

Castenholz, R. W. 1963. An experimental study of the vertical distribution of littoral marine diatoms. Limnol. Oceangr. 8(4):450–463.

———. 1964. The effect of daylight and light intensity on the growth of littoral marine diatoms in culture. Physiol. Pl. 17:951–963.

———. 1967. Seasonal ecology of non-planktonic marine diatoms on the western coast of Norway. Sarsia 29:237–256.

Castracane, A. F. 1875. Contribuzione alla florula delle Diatomee del Mediterraneo, etc. Atti Accad. "Nuovi Lincea" 28:377–396.

Cholnoky, B. J. 1968. Die Okologie der Diatomeen in Binnengewassern. Verlag von J. Cramer, Lehre. 699 pp.

Cleve, P. T. 1873. On diatoms from the Arctic Sea. Bih. K. Svenska Vetensk.-Akad. Handl. 1(13):1–28.

———. 1878. Diatoms from the West Indian archipelago. Bih. Till kongl. Svenska Vetensk.-Akad. Handl. 5(8):1–22.

———. 1881. On some new and little-known diatoms. Bih. K. Svenska Vetensk.-Akad. Handl. 18(5):1–28.

———. 1891. Diatomées rare ou nouvelles. Le Diatomiste 1:75–78.

———. 1894*a*. Planktonundersokningar. Cilioflagellater og Diatomaceer. Bih. K. Svenska Vetensk.-Akad. Handl., vol. 20, part 3, No. 2, 16 pp.

———. 1894*b*. Synopsis of the naviculoid diatoms, Part I. Bih. K. Svenska Vetensk.-Akad. Handl. 26(2):1–194.

———. 1895. Synopsis of the naviculoid diatoms, Part II. Bih. K. Svenska Vetensk.-Akad. Handl. 27(3):1–219.

———. 1896. Diatoms from Baffin Bay and Davis Strait. Bih. K. Svenska Vetensk.-Akad. Handl. 22(4):1–22.

———. 1904. Plankton table for the North Sea. Bull. Cons. Explor. Mer. 1903–1904:216.

Cleve, P. T. and Grunow, A. 1880. Beitrage zur Kenntnis der Arktischen Diatomeen. Bih. K. Svenska Vetensk.-Akad. Handl. 17(2):1–121.

Cleve-Euler, A. 1951. New contributions to the Diatomaceous flora of Finland. Ark. Bot. 14:1–81.

———. 1952. Die Diatomeen von Schweden und Finnland. K. Svenska Vetensk.-Akad. Handl. Series 4, 3(3):1–153 (part V, Schluss.).

———. 1953. Die Diatomeen von Schweden und Finnland. K. Svenska Vetensk.-Akad. Handl. Series 4, 4(5):1–255 (part III, Monoraphideae, Biraphideae I).

Cloern, J. E. 1979. Phytoplankton ecology of the San Francisco Bay system: the status of our current understanding. Pp. 247–264 *in* San Francisco Bay: the urbanized estuary. T. J. Conomos, ed. Pacific Division, American Association for the Advancement of Science, San Francisco, California.

Cohn, F. 1878. "Kryptogamen-Flora von Schlesien." Band 2, erste Halfe J.U. Kern, Breslau. 2845 pp.

Colijn, F. and K. S. Dijkema 1981. Species composition of benthic diatoms and distribution of chlorophyll *a* on an intertidal flat in the Dutch Wadden Sea. Mar. Ecol. Prog. Ser. 4:9–21.

Colijn, F. and H. Nienhuis. 1978. The intertidal microphytobenthos of the "Hohe Weg" shallows in the German

Wadden Sea. Forsch.-Stelle f. Insel:u. Kustenschutz, Norderney, Jahresbericht 1977, 24:149–174.

Conomos, T. J., ed. 1979. San Francisco Bay: the urbanized estuary. Pacific Division, American Association for the Advancement of Science, San Francisco, California. 493 pp.

Cook, L. L. and S. A. Whipple. 1982. The distribution of edaphic diatoms along environmental gradients of a Louisiana salt marsh. J. Phycol. 18:64–71.

Cox, E. J. 1979. Taxonomic studies on the diatom genus *Navicula* Bory: The typification of the genus. Bacillaria 2: 137–152.

Crawford, R. M. 1975. The taxonomy and classification of the diatom genus *Melosira* C. Ag. I. The type species *M. nummuloides* C. Ag. British Phycol. J. 10:323–338.

———. 1977. The taxonomy and classification of diatom genus *Melosira* C. Ag. II. *M. moniliformis* (Mull) C. Ag. Phycologia 16:277–85.

———. 1979. Taxonomy and frustular structure of the marine centric diatom *Paralia sulcata*. J. Phycol. 15:200–210.

Cupp, E. E. 1943. Marine plankton diatoms of the west coast of North America. Bull. Scripps Inst. Oceanogr. (Univ. California, La Jolla) 5:1–238.

Desmazieres, J. B. H. T. 1825. Plantes cryptogames de la France. 1st ed. Lille.

Dixon, W. J., ed. 1981. BMDP Statistical Software. University of California Press, Berkeley, California. 725 pp.

Donkin, A. S. 1861. On the marine Diatomaceae of Northumberland, with a description of several new species. Q. J. Micros. Sci., N.S. 1:1–15.

Ehrenberg, C. G. 1832. Entwicklung und Lebensdauer der Infusionsthiere. Abh. Akad. Wiss. Berlin, 1831. 1–154 pp.

———. 1837. Uber ein fossilen Infusorien bestehendes, 1832 zu Brod verbacknes Bergmehl von der Grenzen Lapplands in Schweden. Bericht uber die zur Bekanntmachung geeigneten Verhandlungen der konigl. preuss. Akad. Wiss. Berlin. Pp. 43–45.

———. 1838. Die Infusionsthierchen als vollkommende Organismen. Ein Blick in das tiefere organische Leben der Natur. Leopold Voss, Leipzig. i–xvii + 1–548 pp.

———. 1839. Uber noch jetzt zahlreich lebende Thierarten der Kreildebildung und den Organismus der Polythalmien. Abh. Adad. Wiss. Berlin (1841), S. 81–174.

———. 1840. Uber ausgezeichnete jetzt lebende peruanische und mexikanische Meeres-Infusorien, welche mit zur Erlauterung rathselhaften fossiler Formen der Kreidebildung dienen. Bericht uber die zur Bekanntmachung geeigneten Verhandlungen der konigl. preuss. Akad. Wiss. Berlin (1841), S. 197–219.

———. 1841. Verbreitung und Einfluss des mikroskopischen Lebens in Sud- und Nord-Amerika. Abh. konigl. Acad. Wiss. Berlin (1843). Theil I, S. 291–445.

———. 1843. Uber (seine) fortgesetzte Beobachtungen des bedeutenden Einflusses unsichtbar kleiner Organismen auf die unteren Stromgebiethe, besonders der Elbe, Jahde, Ems, und Schelde. Bericht uber die zur Bekanntmachung geeigneten Verhandlungen der konigl. preuss. Akad. Wiss. Berlin, S. 259–272.

———. 1844. Mittheilung uber 2 neue Lager von Gebirgsmassen aus Infusorien als Meeres-Absatz in Nord-Amerika und eine Vergleichung derselben mit den organischen Kreide-Gebilden in Europa und Afrika. Bericht uber die zur Bekanntmachung geeigneten Verhandlungen der konigl. preuss. Akad. Wiss. Berlin, S. 57–97.

———. 1845. Vorlaufige zweite Mettheilung uber kie Beziehungen des kleinsten organischen Lebens zu den vulkanischen Massen der Erde. Bericht uber die zur Bekanntmachung geeigneten Verhandlungen der konigl. preuss. Akad. Wiss. Berlin, S. 133–157.

———. 1854. Mikrogeologie das Erden and Felsen schaffende wirken des unsichtbar kleinen selbstandigen Lebens auf der Erde. Leipzig.

Frane, J. W. and M. Hill. 1976. Factor analysis as a tool for data analysis. Commun. Statist.-Theor. Math. 6:487–506.

Frenguelli, J. 1953. Diatomeas del Territorio Nacional de Misiones. Revista del Museo de la Cindad Eva Peron, Nueva Serie, Seccion Botanica 8:63–86.

Fricke, F. 1904. Schmidt's Atlas der Diatomaceen-Kunde. Tafeln 247–256. R. Reisland, Leipzig.

Fryxell, G. A. 1975. Three new species of *Thalassiosira* with observations on the occluded process, a newly observed structure on diatom valves. Nova Hedwigia Beihefte 53:57–80.

Fryxell, G. A. and G. R. Hasle. 1972. *Thalassiosira eccentrica* (Ehrenb.) Cleve, *T. symmetrica* sp. nov., and some related centric diatoms. J. Phycol. 8:297–317.

Fryxell, G. A. and W. I. Miller. 1978. Chain-forming diatoms: three araphid species. Bacillaria 1:113–136.

Germain, H. 1979. Details of structure in three small freshwater *Diploneis*. Nova Hedwigia Beihefte 64:207–217.

Giffen, M. H. 1970*a*. Contributions to the diatom flora of South Africa IV. The marine littoral diatoms of the estuary of the Kowie River, Port Alfred, Cape Province. Nova Hedwigia Beihefte 31:259–312.

———. 1970*b*. New and interesting marine and littoral diatoms from Sea Point, New Cape Town, South Africa. Bot. Mar. 14:89–99.

———. 1971. Marine littoral diatoms from the Gordons Bay region of False Bay, Cape Province, South Africa. Bot. Mar. 14:1–16.

———. 1973. Diatoms of the marine littoral of Steenbergs Cove in St. Helena Bay, Cape Province, South Africa. Bot. Mar. 16:32–48.

———. 1975. An account of the littoral diatoms from Langebaan, Saldanha Bay, Cape Province, South Africa. Bot. Mar. 18:71–95.

Gmelin, J. F. 1788. *Bacillaria paradoxa in* Linnaeus, "Systema Naturae," 13th ed. Vol. 1, pars. 6, no. 3903.

Gran, H. H. 1897. Bacillariaceen vom Kleinen Karajakfjord. Bibliotheca Botanica, Stuttgart. Heft 42, S. 1–24.

Gran, H. H. and E. C. Angst. 1931. Plankton diatoms of Puget Sound. Publications of the Puget Sound Biological Station (Univ. Washington) 7:417–519.

Gray, S. F. 1821. A natural arrangement of British plants. London.

Gregory, W. 1856. On the post-tertiary diatomaceous sand of Glenshira. Trans. Micros. Soc. Lond. n.s. 4:35–48.

———. 1857. On new forms of marine Diatomaceae found in the Firth of Clyde and in Loch Fyne, illustrated by numerous figures drawn by R. Greville, LL.D., F.R.S.E. Trans. R. Soc. Edinburg 21:473–452.

Greville, R. K. 1859. Descriptions of some new diatomaceous forms from the West Indies. Q. J. Micros. Sci. 5:7–12.

———. 1861. Descriptions of new and rare diatoms. Trans. Micros. Soc. Lond. n.s. 9(II):67–73.

———. 1865. Descriptions of new and rare diatoms. Ser. 14. Trans. Micros. Soc. Lond. n.s. 13:1–10.

Griffith, J. W. and Henfrey, A. 1856. Diatomaceae in

"The micrographic dictionary," 1st ed. John VanVoorst, Paternoster Row, London.

GRUNOW, A. 1860. Uber neue oder ungenugend bekannte Algen. Diatomeen. Verh. zool-bot. Ges. Wien 10:503–582.

———. 1862. Die osterreichischen diatomaceen nebst anchluss einiger neuen arten von andern lokalitaten und einer kritischen uebersicht der bisher bekannten gattungen und arten. Verh. zool-bot. Ges. Wien 12:315–472, 545–585.

———. 1863. Uber einige neue und ungenugend bekannte Arten und Gattungen von Diatomaceen. Verh. zool-bot. Ges. Wien 13:137–62.

———. 1868*a*. Beitrage zur Kenntriss der Schizonema—und Berkeleya—Arten. Hedwigia, Bd. 7, Nr. 1, 1–7, etc.

———. 1868*b*. Algae in "Reise der osterreichschen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859." Botan. Theil (1) S. 1–104. Taf. 1–11.

———. 1878. Algen und Diatomaceen ausdem Kapischen Meere. Naturwiss. Beitr. Kennt.d. Kaukasuslander (Schneider). Pp. 98–132.

———. 1879. New species and varieties of Diatomaceae from the Caspian Sea. J. R. Micros. Soc. 2:677–91.

———. 1880. On some new species of *Nitzchia*. J. R. Micros. Soc. 3:394–397.

———. 1881. Botanis. Centralblatt, Bd 8.

HAGELSTEIN, R. 1939. The Diatomacea of Puerto Rico and the Virgin Islands. New York Academy of Sciences, Survey of Porto Rico and the Virgin Islands 8(3):313–450.

HAKANSSON, H. 1979. Examination of diatom type material of C. A. Agardh. Nova Hedwigia Beihefte 64:163–168.

HARPER, C. W., JR. 1978. Groupings by locality in community ecology and paleoecology: tests of significance. Lethaia 11:251–257.

HASEGAWA, Y. 1975. Significance of diatom thanatocoenoses in the neolithic sea-level change problem. Pac. Geol. 10:47–78.

HASLE, G. R. 1977. Morphology and taxonomy of *Actinocyclus normanii* f. *subsalsa* (Bacillariophyceae). Phycologia 16(3):321–328.

———. 1979. *Thalassiosira decipiens* (Grun.) Jorg. (Bacillariophyceae). Bacillaria 2:85–108.

———. 1983. *Thalassiosira punctigera* comb. nov., a widely distributed planktonic diatom. Nordic J. Bot. 3:593–608.

HASLE, G. R. AND G. A. FRYXELL. 1977. The genus *Thalassiosira:* some species with a linear areola array. Nova Hedwigia Beihefte 54:15–66.

HASLE, G. R. AND B. R. E. DE MENDIOLA. 1967. Fine structure of some *Thalassionema* and *Thalassiothrix*. Phycologia 6: 107–125.

HASSALL, A. H. 1845. A history of the British freshwater algae (including descriptions of the Diatomaceae) with upwards of one hundred plates. Taylor, Walton, and Maberly, London. Vol. 1, 462 pp. text. Vol. 2, 103 plates.

HEIBERG, P. A. C. 1863. Conspectus criticus Diatomacearum Danicarun. Wilhelm Priors Forlag, Kjobenhaun. 135 pp.

HENDEY, N. I. 1951. Littoral diatoms of Chichester Harbor with special reference to fouling. J. R. Micros. Soc. 71:1–86.

———. 1953. Taxonomic studies on some *Naviculae Punctatae*. J. R. Micros. Soc. 73:156.

———. 1958. Marine diatoms from some West African ports. J. R. Micros. Soc. 77:28–85.

———. 1964. An introductory account of the smaller algae of the British coastal waters. Part 5: Bacillariophyceae (Diatoms), Ministry of Agriculture, Fisheries and Food, Fishery Investigations Series 4. Her Majesty's Stationary Office, London. 317 pp.

———. 1970. Some littoral diatoms of Kuwait. Nova Hedwigia Beihefte 31:107–167.

HUSTEDT, F. 1914. Bacillariales aus den Sudeten und einigen benach—barten Gebieten des odertales. Archiv fur Hydrobiologie und Planktonkunde, Bd. 10, S. 1–65, Taf. 2.

———. 1921. Zellpflanzen ostafrikas, gesammelt auf der akademischen studienfahrt. 1910 von Bruno Schroder VI. Bacillariales. Hedwigia, Band 63, S. 117–173. Taf. 1.

———. 1927. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 1, S. 1–272 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

———. 1928. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 1, S. 273–464 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

———. 1929. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 1, S. 465–608 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

———. 1930*a*. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 1, Lief 4–5, S. 609–920 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

———. 1930*b*. Bacillariophyta (Diatomeae), Vol. 10 *in* Pascher, A., ed., Die Susswasser-Flora Mitteleuropas. Jena, Gustav Fisher. 466 pp.

———. 1931. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 2, S. 1–176 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

———. 1932. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 2, S. 177–320 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

———. 1933. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 2, Lief 3–4, S. 321–576 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

———. 1934. Die Diatomeenflora von Poggenpohls Moor bei Dotlingen in Oldenburg. Abhandl. und Vortragen der Breman Wissen schaftlichen Gesellshaft, Jahrgang 8/9, S. 362–403.

———. 1937. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 2, S. 577–736 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

———. 1939. Die Diatomeenflora des Kustengebietes der Nordsee vom Dollart bis zur Elbe—mundung. Abh. Naturw. Ver. Bremen 31:572–677.

———. 1944. Neue und wenig bekannte Diatomeen. Ber. Dtsch. Bot. Ges. 61:211–90.

———. 1954. Neue und wenig bekannte Diatomeen. VI. Ber. Dtsch. Bot. Ges. 67:269–280.

———. 1955. Marine littoral diatoms of Beaufort, North Carolina. Bull., Duke Univ. Mar. Stn. No. 6.

———. 1957. Die Diatomeenflora des Flusssystems der Wes-

er in Gebiet der Hansestadt, Bremen. Abh. Naturw. Ver. Bremen 34:181–440.

———. 1959. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 2, S. 737–845 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

———. 1961. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 3, S. 1–160 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

———. 1964. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 3, S. 349–556 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

———. 1966. Die Kieselalgen Deutschland, Oesterreich und der Schweiz mit Beruchsichtigung der ubringen Lander Europas sowie der angrenzeden Meeresgebiete. Band 7, Teil 3, S. 557–816 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz.

Jorgensen, E. 1905. Protist plankton. The protist plankton and the diatoms in bottom samples. Hydrographical and biological investigations in Norwegian fjords. Bergens Mus. Skr. 7:49–148.

Jousé, A. P. 1962. Stratigraphische und palaeogeographische Untersuchungen im Nordwestteil des Pazifik. Verlag Akad. Wiss. USSR, 5 Moscow.

Kitton, F. 1869. Notes on New York Diatoms with description of a new species *Fragilaria crotonensis.* (K. Hardwicke's) Science Gossip 5:109–110.

Krasske, G. 1927. Diatomeen deutscher solquellen und Gradierwerke. Archiv fur Hydrobiologie 18:252–272.

Krone, R. B. 1979. Sedimentation in the San Francisco Bay System. Pp. 85–96 *in* San Francisco Bay: the urbanized estuary. T. J. Conomos, ed. Pacific Division, American Association for the Advancement of Science, San Francisco, California.

Kutzing, F. T. 1833. Synopsis Diatomearum. Linnaea 8: 529–620.

———. 1844. Die Kieselschaligen Bacillarien oder Diatomeen. Nordhausen.

———. 1846. Kurze Mittheilung uber einige Kieselschalige Diatomeen. Botan. Zeitung, Bd. 4, S. 247–248.

———. 1849. Species Algarum. F. A. Brockhaus, Leipzig. 922 pp.

Lagerstedt, N. G. W. 1873. Sotvattens-Diatomaceer fran Spetsbergen och Beeren Eiland. Bih. K. Svenska Vetensk.-Akad. Handl. 1(14):1–52.

Lange-Bertalot, H. 1977. Eine Revision zur Taxonomie der *Nitzschiae lanceolatae* Grunow: Die "Klassichen" bis 1930 beschriebenen Susswasserarten Europas. Nova Hedwigia 28:253–307.

———. 1980*a*. Zur taxonomischen Revision einiger okologish wichtiger "Navicula lineolatae" Cleve: Die Formenkreuse um *Navicula lanceolata, N. viridula,* und *N. cari.* Cryptogamie: Algologie 1:29–50.

———. 1980*b*. Zur systematischen Bewertung der bandformigen Koloniew bei *Navicula* und *Fragilaria.* Nova Hedwigia 33:723–788.

Lange-Bertalot, H. and R. Simonsen. 1978. A taxonomic revision of the *Nitzschiae lanceolatae* Grunow, 2: European and related extra-European freshwater and brackish water taxa. Bacillaria 1:11–111.

Laws, R. A. 1982. Biostratigraphic and paleoenvironmental applications of diatoms in coastal sediments. Abstracts, VII International Symposium on Recent and Fossil Diatoms. Academy of Natural Sciences, Philadelphia.

———. 1983*a*. Preparing strewn slides for quantitative microscopical analysis: a test using calibrated microspheres. Micropaleontology 29:60–65.

———. 1983*b*. Quaternary diatom floras and Pleistocene paleogeography of San Francisco Bay. Ph.D. Dissertation (unpubl.), Univ. of California, Berkeley, California. 350 pp. 35 pl.

Lewis, F. W. 1862. Notes on new and rare species of Diatomaceae of the United States seaboard. Proc. Acad. Nat. Sci. Phila. 1861, pp. 61–71.

Lyngbye, H. C. 1819. *Tentamen Hydrophytologiae Danicae.* Copenhagen. 248 pp.

Mahood, Á. D., G. A. Fryxell, and M. McMillan. 1986. The diatom genus *Thalassiosira*: species from the San Francisco Bay area. Proc. Calif. Acad. Sci. 44:127–156.

Main, S. P. and C. D. McIntire 1974. The distribution of epiphytic diatoms in Yaquina Estuary, Oregon (U.S.A.). Bot. Mar. 17:88–99.

McIntire, C. D. 1978. The distribution of estuarine diatoms along environmental gradients: a canonical correlation. Estur. Coastal Mar. Sci. 6:447–457.

McIntire, C. D. and W. S. Overton. 1971. Distributional patterns in assemblages of attached diatoms from Yaquina Estuary, Oregon. Ecology 52:758–777.

McIntire, C. D. and C. W. Reimer. 1974. Some marine and brackish water *Achnanthes* from Yaquina Estuary, Oregon (U.S.A.). Bot. Mar. 17:164–175.

Meister, F. 1912. Die Kieselalgen der Schweiz. Beitrage zur Kryptogamenflora der Schweiz. Wyss, Bern. Band IV, Heft 1, S. 254, Taf. 48.

———. 1935. Seltene und neue Kieselalgen. I. Berichte der Schweizerischen Botanischen Gesellschaft Bd. (Heft) 47, S. 258–276, Taf. 3–13.

Mertz, D. 1966. Mikropalaeontologische und sedimentologische Untersuchung der Pisco-Formation Sudperus. Palaeontographica, Abt. B 118, 1.

Miller, U. 1964. Diatom floras in the Quaternary of the Gota River valley. Sveriges Geologiska Undersokning, No. 44.

Moghadam, F. 1969. An ecological and systematic study of the planktonic diatom communities in Flathead lake, Montana. Proc. Acad. Nat. Sci. Phila. 121(6):153–228.

Moore, M. S. 1843. No Title *in* J. Ralfs, On the British Diatomaceae. Ann. Mag. Nat. Hist. 1843:346–352.

Morrison, D. F. 1976. Multivariate statistical methods, 2nd ed. McGraw Hill, New York. 415 pp.

Müller, O. 1893. Die Ortsbewegung der Bacillariaceen betreffend. Ber. Dtsch. Bot. Ges. 11:571–600.

———. 1895. Rhopalodia, ein neues Genus der Bacillariaceen. Engler Bot. Jahrb. 22:54–71.

Neff, N. A. and L. F. Marcus. 1980. A survey of multivariate methods for systematics for a workshop: Numerical methods in systematic mammalogy. Am. Soc. Mammal. Ann. Mtg. Am. Mus. Nat. Hist., New York.

Norman, G. 1861. On some undescribed species of Diatomaceae. Trans. Micros. Soc. Lond., n. s. 9:5–9.

Ostenfeld, C. H. 1915. A list of phytoplankton from the Boeton Straight, Celebes. Dansk. bot. Art. Vol. 2, No. 4, Copenhagen.

Pankow, H. 1976. Algenflora der Ostsee, II Plankton. Fischer, Stuttgart.

PANTOCSEK, J. 1889. Beitrage zur Kenntnis der fossilen Bacillarien Ungarns. Teil II. Brackwasser Bacillarien. Anhang: Analyse der marine Depots von Bory, Bremia, Nagy-Kurtos in Ungarn; Ananio und Kusnetzk in Russland. Nagy-Tapolcsany. Julius Platzko. 123 pp.

———. 1892. Beitrage zur Kenntnis der fossilen Bacillarien Ungarns. Teil III. Susswasser Bacillarien. Anhang-analysen 15 neuer Depots von Bulgarien, Japan, Mahren, Russland und Ungarn. Nagy-Tapolcsany. Julius Platzko. 118 pp.

———. 1902. Kieselalgen oder Bacillarien des Balaton (Plattensees), "Resultate der wissenschaftlichen Erforschung des Balatonsees." Herausgegeben von der Balatonsee-Commission der Ung. geographischen Gesellschaft, Wien. Zweiter Band, zweiter Theil, Sec. I, Anhang. 112 pp.

PATRICK, R. 1959. New species and nomenclatural changes in the genus *Navicula* (Bacillariophyceae). Proc. Acad. Nat. Sci. Phila. 111:91–108.

PATRICK, R. AND C. W. REIMER. 1966. The diatoms of the United States—exclusive of Alaska and Hawaii. Acad. Nat. Sci. Phila., Monograph 13, vol. 1. 688 pp.

———. 1975. The diatoms of the United States—exclusive of Alaska and Hawaii. Acad. Nat. Sci. Phila., Monograph 13, vol. 2, part 1. 213 pp.

PELLETAN, J. 1889. Les Diatomées histoire naturelle, préparation classification et description des principales espèces. J. Micrographie II:1–364.

PERAGALLO, H. AND M. PERAGALLO. 1897–1908. Diatomées marines de France et des districts maritimes voisins. Micrographe-Editeur, a Grez-sur-Loing. 491 pp. + 41 pp. Atlas. 137 pl. (pl. 1–24, 1897; pl. 25–48, 1898; pl. 48–72, 1899; pl. 73–80, 1900; pl. 81–96, 1901; pl. 97–110, 112–113, 1902; pl. 124–131, 1904; pl. 132–135, 1905; pl. 120–124, 136–137, 1907; pl. 111, 114–119, 1908).

PETERSON, C. H. 1979. Predation, competitive exclusion, and diversity in soft-sediment benthic communities of estuaries and lagoons. Pp. 233–263 *in* Ecological processes in coastal and marine systems. R. J. Livingston, ed. Plenum Publishing Corp., New York.

PETERSON, D. H., T. J. CONOMOS, W. W. BROAKOW, AND P. C. DOHERTY. 1975. Location of the nontidal current null zone in Northern San Francisco Bay. Estur. Coastal Mar. Sci. 3:1–11.

PETIT, P. 1877. Liste des diatomées et des desmidiees observees dans les environs de Paris precedee d'un classification des diatomées. Extraits du Bull. de la Societe botanique de France 24:1–32.

———. 1888. Diatomacees recoltees dans le voisinage du Cap Horn. Mission Sci. du Cap Horn, 1882–1883, 5(Bot.): 111–140. Paris.

PFITZER, E. 1871. Untersuchungen uber Bau und Entwicklung der Bacillariaceen (Diatomaceen). Hanstein's Bot. Abh. 2:1–189.

PRITCHARD, A. 1861. A history of the Infusoria, including the Desmidiaceae and Diatomaceae, British and Foreign. 4th ed. London. Diatoms by J. Ralfs, pp. 756–947.

RABENHORST, L. 1848–1860. Die Algen Sachsens. Resp. Mittel-Europa's Gesammelt und herausgegeben von Dr. L. Rabenhorst Dec. 1–100. Algen Europa's Dec. 1–104 (101–204), Nos. 1–1000. Exsiccata (issued at various dates). Dresden.

———. 1853. Die Susswasser Diatomaceen (Bacillarien) fur Freunde der Mikroskopie. Eduard Kummer, Leipzig. 72 pp.

———. 1861–1879. Die Algen Europa's. Forsetzung der Algen Sachsens. Resp. Mittel-Europa's Nos. 1001–2590. Dec. 1–257. Exsiccata. Dresden.

RALFS, J. 1843. On the British Diatomaceae. Ann. Mag. Nat. Hist. 1843:346–352. (or II:447–457.)

REASIDE, J. D. 1970. Note on the occurrence of the diatoms *Cymbella jordani* Grun ex Cleve and *Eunotia serpentina* Ehr. in New Zealand. Nova Hedwigia Beihefte 31:537–542.

ROSS, R. 1947. Fresh water Diatomaceae (Bacillariophyta) Vol. II *in* Botany of the Canadian Eastern Arctic, N. V. Polunin, ed. Bull. Nat. Mus. Canada 97:178–233.

ROUND, F. E. 1971. Benthic marine diatoms. Oceangr. Mar. Biol. Ann. Rev. 9:83–139.

SCHMID, A. 1977. Morphologische und physiologische untersuchungen an diatomeen des neusiedler—sees; II Licht und rasterelektronnenmikroskopische schalenanalyse der umwellabhangig Zyklomophose von *Anomoeneis sphaerophora* (K. G.) Pfitzer. Nova Hedwigia 28:309–351.

SCHMIDT, A. 1874–1959. Atlas der Diatomaceen-Kunde. Heft 1–120, Taf. 1–472 (Taf. 1–216 A. Schmidt; 213–216, 1899, M. Schmidt; 217–240, 1900–1901, F. Fricke; 241–244, 1903, H. Heiden; 245–246, 1904, O. Müller; 247–256, 1904–1905, F. Fricke; 257–264, 1905–1906, H. Heiden; 265–268, 1906, F. Fricke; 268–472, 1911–1959, F. Hustedt). R. Reisland, Leipzig.

SCHMIDT, M. 1899. Schmidt's Atlas der Diatomaceen-Kunde. R. Reisland, Leipzig. Taf. 213–216.

SCHRADER, H.-J. 1973. Cenozoic diatoms from the Northeast Pacific, Leg. 18. Initial Reports, Deep Sea Drilling Project 18:673–797.

———. 1978. Quaternary through Neogene history of the Black Sea, deduced from the paleoecology of diatoms, silicoflagellates, ebridians, and chrysomonads. Initial Reports, Deep Sea Drilling Project 42-B:789–901.

SCHRADER, H.-J. AND R. GERSONDE. 1978. Diatoms and silicoflagellates. Utrecht Micropaleontol. Bull. 17:129–176.

SCHUETTE, G. AND H.-J. SCHRADER. 1979. Diatom taphocoenoses in the coastal upwelling area off western South America. Nova Hedwigia Beihefte 64:359–378.

———. 1981. Diatom taphocoenoses in the coastal upwelling area off south west Africa. Mar. Micropaleontol. 6:131–155.

SCHULZ, P. 1926. Die Kieselalgen der Danziger Bucht mit Einschluss derjenigen aus glazialen und postglazialen Sedimenten. Botan. Arkiv. 13:149–327.

SETTY, M. G. A. P. 1966. Preparation and method of study of fossil diatoms. Micropaleontology 12:511–514.

SIMONSEN, R. 1962. Untersuchungen zur systematik und Okologie der Bodendiatomeen der westlichen Ostsee. Int. Rev. ges. Hydrobiol. (syst. Beih.) 1:9–144.

———. 1979. The diatom system: Ideas on phylogeny. Bacillaria 2:9–71.

SITTS, R. M. AND A. W. KNIGHT. 1979. Plankton ecology in the Sacramento–San Joaquin Estuary. Dept. of Land, Air and Water Resources, Univ. Calif., Davis, Water Science and Engineering Papers No. 4509.

SKVORTZOW, B. W. AND MAYER, C. I. 1928. A contribution to the diatoms of Baikal Lake. Proc. Sungaree River Biol. Stn. 1(5):1–55.

SLOAN, D. 1981. Ecostratigraphic study of Sangamon sediments beneath central San Francisco Bay. Ph.D. Dissertation (unpubl.), Univ. of California, Berkeley, California. 316 pp.

SMITH, WM. 1851. Notes on the Diatomaceae with descriptions of British species included in the genera campylodiscus, Surirella, and Cymatopleura. Ann. Mag. Nat. Hist. 7.

———. 1852. Notes on the Diatomaceae; with description of British species included in the genus Pleurosigma. Ann. Mag. Nat. Hist. 9:1–12.

———. 1853. Synopsis of British Diatomaceae, vol. I. John Van Voorst, London. 89 pp.

———. 1856. Synopsis of British Diatomaceae, vol. II. John Van Voorst, London. 107 pp.

Sneath, P. H. A. and R. R. Sokal. 1973. Numerical taxonomy: the principles and practices of numerical classification. W. H. Freeman, San Francisco, California.

Sovereign, H. E. 1958. The diatoms of Crater Lake, Oregon. Trans. Am. Micros. Soc. 77:96–134.

Stoermer, E. F. and J. J. Yang. 1969. Plankton diatom assemblages in Lake Michigan. Univ. Mich., Spec. Rep., Great Lakes Res. Div., Ann Arbor 47:1–268.

Storrs, P. N., R. E. Selleck, and E. A. Pearson. 1966. Summary of physical, chemical and biological water and sediment data. Univ. Calif., Berkeley, Sanitary Engineering Res. Lab., Rep. No. 67-2. 140 pp.

Sullivan, M. J. 1982. Distribution of edaphic diatoms in a Mississippi salt marsh: a canonical correlation analysis. J. Phycol. 18:130–133.

Temperé, J. and M. Peragallo. 1910. Diatomées du monde entire, 2nd ed. Arcachon, Grez-sur-loing. Pp. 209–256.

Thompson, J. K. and R. A. Laws. 1982. Seasonal patterns in benthic microalgae biomass and species composition in San Francisco Bay. Abstract, Proceedings, Tenth Meeting, Pacific Estuarine Research Society, San Francisco, California. Addendum.

Thompson, J. K., F. Nicols, and S. Wienke. 1981. Distribution of benthic chlorophyll in San Francisco Bay, California, February 1980–February 1981. U.S. Geol. Sur., Open File Report 81-1134.

Thwaites, G. H. K. 1848. Further observations on the Diatomaceae with descriptions of new genera and species. Ann. Mag. Nat. Hist. 1(ser. 2):161–172.

Turpin, P. J. F. 1828. Observations sur le nouveau genre *Surirella*. Mem. Mus. Hist. Nat. Paris 16:361–368.

Van Heurck, H. 1880–1885. Synopsis des diatomees de Belgique, Atlas (pl. 1–30, 1880; pl. 31–77, 1881; pl. 78–103, 1882; pl. 104–132, 1883: pl. A, B, C, 1885). Ducaju and Cie., Anvers. Table alphabetique (Index) (1884), J. F. Dieltjens, Anvers, 120 pp. Texte (1885), Mtin. Brouwers & Co., Anvers, 235 pp.

Van Landingham, S. 1967. Catalogue of the fossil and Recent genera and species of diatoms and their synonyms. A revision of F. W. Mills' "An index to the genera and species of the Diatomaceae and their synonyms." Part I, *Acanthoceras-Bacillaria*. J. Cramer, Lehre. 1–493 pp.

———. 1971. Catalogue of the fossil and Recent genera and species of diatoms and their synonyms. A revision of F. W. Mills' "An index to the genera and species of the Diatomaceae and their synonyms." Part IV *Fragilaria-Naunema*. J. Cramer, Lehre. 1087–1756 pp.

———. 1978. Catalogue of the fossil and Recent genera and species of diatoms and their synonyms. A revision of F. W. Mills' "An index to the genera and species of the Diatomaceae and their synonyms." Part VII *Rhoicosphenia-Zygoceros*. J. Cramer, Lehre. 3606–4241 pp.

Wagner, D. B. 1978. Environmental history of central San Francisco Bay with emphasis on foraminiferal paleontology and clay mineralogy. Ph.D. Dissertation (unpubl.), Univ. of California, Berkeley. 247 pp.

Wallich, G. C. 1858. On *Triceratium* and some new allied forms with figures of the same. Q. J. Micros. Sci. 6:242–253.

Weisse, J. F. 1854. Mikroskopischen Analyse eines organischen Ploirschiefers aus dem Gouvernment Simbirsk. Melanges Biologiques tires du Bulletin de l'Academie Imperiale des Sciences de St. Petersbourg 2:237–250.

Wong, R. L. J. 1975. Diatom flora of the phytoplankton of San Francisco Bay. M.S. Thesis (unpubl.), San Francisco State University, San Francisco. 144 pp.

———. 1982. Benthic diatom variation during a tidal cycle: Suisun Bay, California, 28 May 1980. Abstract, VII International Symposium on Recent and Fossil Diatoms, Acad. Nat. Sci. Phila.

Wong, R. L. J. and J. E. Cloern. 1981. Plankton studies in San Francisco Bay. II Phytoplankton abundance and species composition, January 1977–December 1979. U.S. Geol. Surv. Open File Rep. 81-214.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 10, pp. 255–266, 5 figs., 2 tables. April 12, 1988

MARGINAL MARINE PLEISTOCENE FOSSILS FROM NEAR MOUTH OF MAD RIVER, NORTHERN CALIFORNIA

By
William Miller, III
Department of Geology and Marine Laboratory, Humboldt State University, Arcata, California 95521

and
Samuel D. Morrison
1308 Janes Road, Arcata, California 95521

ABSTRACT: Late Pleistocene high-energy nearshore to strand-plain sands and gravels are succeeded by shelly backbar deposits in a cliff exposure near the mouth of Mad River, coastal Humboldt County. Backbar sediments consist of a protected slough-margin sandflat and an overlying muddy-bottom slough-basin facies. Fossil associations from both facies are dominated by mollusks (23 species in all), many of which are in place or only slightly disturbed. The association from the sandflat facies is dominated by balanid barnacles and infaunal suspension-feeding bivalves (*Saxidomus gigantea, Protothaca staminea, Tresus* sp.). Fine-grained slough-basin deposits contain remains of oyster gardens consisting of clumps of *Ostrea lurida* along with barnacles, the ectoparasitic snail *Odostomia nota,* and borings produced by the endolithic polychaete *Polydora* sp.; the intervening muddy matrix surrounding oyster clumps contains *P. staminea* and the infaunal deposit-feeding bivalve *Macoma nasuta.*

Received May 20, 1987. Accepted September 29, 1987.

INTRODUCTION

In January and February 1986, a series of winter storms caused coastal erosion in Humboldt County, California, with high water and extensive bank erosion along the lower reaches of the Mad River. The storms produced a new exposure of Pleistocene sediments in bluffs at the mouth of the river, located 1 km southwest of Arcata Airport (Fig. 1, 2). Near the top of the fresh exposure we found two fossiliferous beds containing many untransported shallow marine and estuarine mollusks. In this paper we describe the fossil deposits and relate them to original depositional environments and benthic communities.

This site is one of few low-energy late Pleistocene marine fossil localities in northern California, north of the type area of the Hookton Formation, consisting largely of well-preserved, autochthonous bivalve and gastropod shells. The excellent state of in situ preservation, with many infaunal and epifaunal-cemented bivalves still in life orientations, permits reconstruction of original community composition and structure, and the documentation of benthic ecology of Hookton (or Falor) Formation equivalents in the mouth of the Mad River area. We studied both the large, conspicuous mollusks typically reported in regional stratigraphic studies as well as diminutive species usually overlooked when isolated localities are sampled by merely hand-picking surface

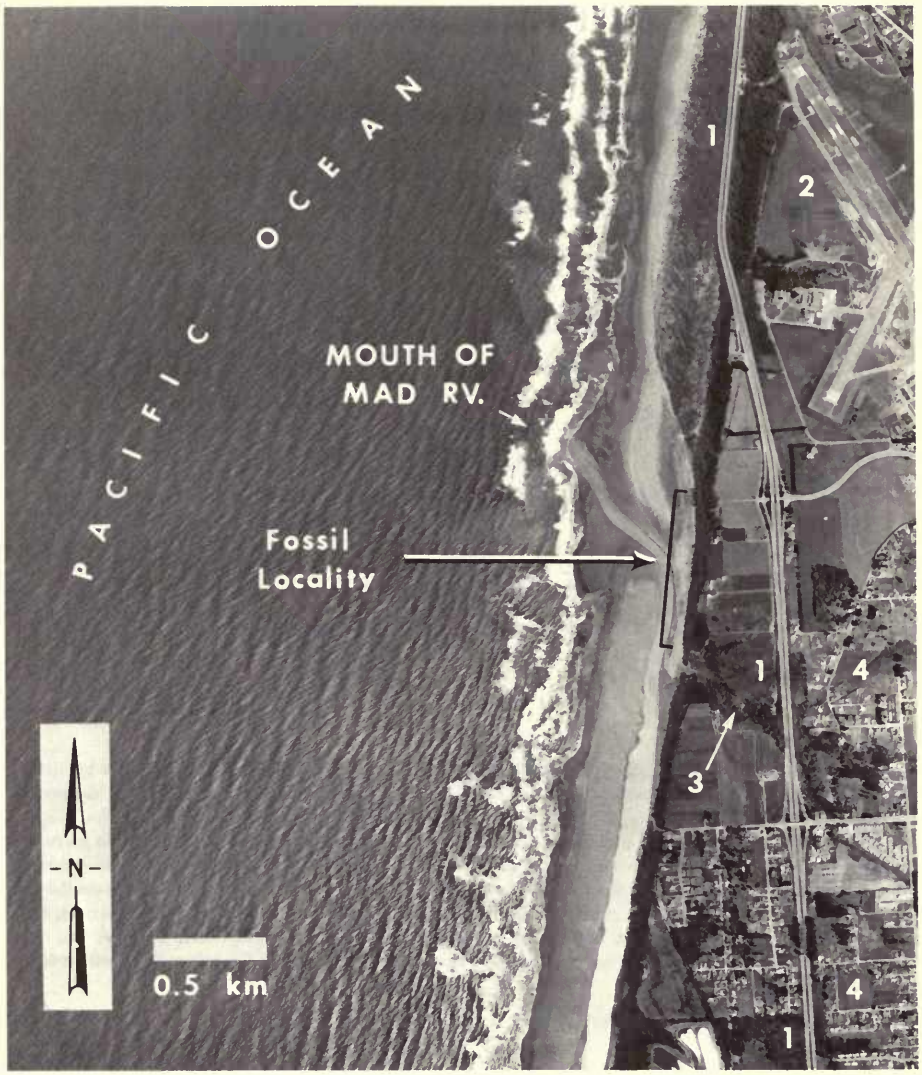


FIGURE 1. Aerial photograph taken in 1984 showing the fossil locality and the following landmarks: (1) U.S. Highway 101; (2) Arcata Airport on the surface of Dows Prairie; (3) Widow White Creek; and (4) town of McKinleyville.

exposures. Accurate estimates of species richness and relative abundance of mollusks were achieved by bulk sampling at our study site.

Bulk sampling allows retrieval of small mollusks that are seldom mentioned in the paleontologic literature and are not well known from modern environments. These components of fossil deposits, although poorly known and sometimes difficult to determine to species (e.g., Pyramidellidae), should not be ignored. They were integral members of original benthic communities and may represent the only preserved evidence of biotic interactions such as parasitism. From a stratigraphic perspective, these smaller mollusks are untested as zonal guide fossils, taking into account the probability that many are restricted to particular sedimentary facies. They are essentially unexploited as stratigraphic guides, yet many occur in large numbers and could be sampled by subsurface methods.

Significantly, the two fossiliferous beds that we studied had sedimentologic and paleoecologic characteristics indicating deposition at or only slightly below paleo-sea level. In an area and time

FIGURE 2. Fossil locality as it appeared in March, 1986. The two fossiliferous beds are located at the level between white arrows; scale indicated by shovel, which is about 1.5 m long.

interval when tectonics, sediment supply, and glacio-eustatic fluctuations were producing rapidly changing, environmentally varied coastal landscapes, such marginal marine beds with their near-sea level biota of oysters and zosteracean plants are important indicators of former shoreline positions. Recognition of such deposits would be useful in studies of coastal uplift rates where an ancient sea level datum is required and age constraints are available.

LOCATION OF SITE AND METHODS

The exposure extends along the bluff line on the east bank of the Mad River, from 100 to 700 m north of the mouth of Widow White Creek along the seaward edge of Dows Prairie (Fig. 1; see also U.S.G.S. Arcata North 7.5′ topographic quadrangle). This lies within the Mad River Fault Zone, which was recently described by Carver (1985) as a northwest-trending zone of crustal

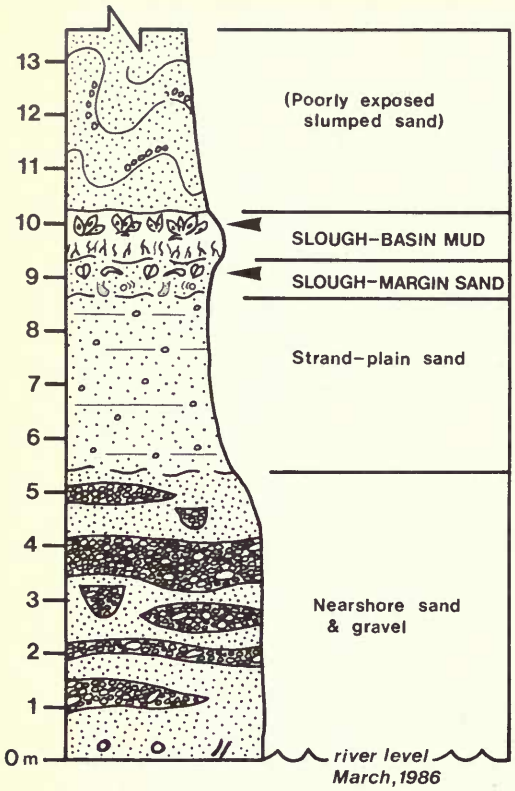


FIGURE 3. Stratigraphic section exposed at mouth of Mad River, showing levels from which samples were collected for paleoecologic analysis (arrows). Section extends upward for at least another 8 m, but is poorly exposed and disrupted by slumping.

compression, thrust faulting, and uplift resulting from convergence of the Gorda and North American plates. Our study site is bounded by the McKinleyville Fault to the north and by a splay of the Mad River Fault to the south (Carver 1985, Fig. 2). Thus, the fossil locality is situated within a fault block and elevation of fossiliferous beds is partly the result of structural uplift.

These two fossil beds occur at a height of between 8.5 and 10.5 m above the level of the river beach (Fig. 2, 3), which is roughly mean sea level (±1 m) near the mouth of the river. This is not the original elevation, however, owing to uplift and tilting of stratigraphic units in the fault zone. At the northern end of the outcrop, approaching the McKinleyville Fault, beds dip 4° to 8° south to southeast and strike generally east–west to northeast. Joints and small reverse faults are clearly visible here. Toward the center of the outcrop bedding gradually becomes horizontal. At the southern end, near Widow White Creek, slumping obscures bedding attitudes. In this area the mud bed shown in Figure 3 appears to be acting as a detachment surface and glide plane, above which the sediments are disrupted by slumping and fracturing.

We collected a total of eight 1-liter bulk samples: three from a bed interpreted as a backbar, slough-margin sandflat deposit and five from an overlying oyster-rich bed that represents a muddy-bottom, slough-basin deposit (Fig. 3). Each sample was soaked in 10% sodium hexametaphosphate solution and washed on a screen with 2-mm openings. All fossils separated from matrix were sorted, identified to species if possible, counted, and examined for epi- and endobionts. Sources consulted in the identification of specimens included: Dall and Bartsch 1909; Oldroyd 1927; Willett 1928; Fitch 1953; Abbott 1974; Keen and Coan 1974; Griffith 1975; Smith and Carlton 1975; Morris et al. 1980; Bernard 1982. Results are summarized in Tables 1 and 2. We noted sedimentary textures, physical and biogenic structures, and geometry of bedding units in the field in order to reconstruct the depositional history of the section.

Stratigraphic Context

REGIONAL SETTING.—The fossil locality is situated in the northern part of the Humboldt Basin, which contains a thick sequence of Late Cenozoic marine and coastal nonmarine sedimentary units (Ingle 1976). Thickness in onshore sections exceeds 3,500 m (Hopps and Horan 1983). The central part of this basin is a north–south-trending trough located on the submerged continental shelf between Cape Mendocino and the California–Oregon border (Hoskins and Griffiths 1971). On land, isolated outcrops of Late Cenozoic beds apparently related to the Humboldt Basin extend from the vicinity of Garberville, southern Humboldt County, to Crescent City in Del Norte County. In the well-known exposures at Centerville Beach and Scotia Bluffs, west-central Humboldt County, thick sections in the basin sequence have been divided into the following formal stratigraphic units, all but the last comprising the Wildcat Group (Ogle 1953): (1) upper Miocene Pullen Formation; (2) Pliocene Eel River Formation; (3) Plio-Pleistocene Rio Dell Formation; (4) Plio-Pleistocene Scotia

TABLE 1. FOSSILS FROM SANDFLAT FACIES (SEE FIG. 3, 5).

Taxa	Average no. individuals/ liter sample* (n = 3)	Standard deviation	Type organism/substrate niche and feeding group†
Autochthonous components (intertidal to shallow subtidal sandy-bottom association)			
Balanus sp.	96.7‡	18.6	Ci/EPSF
Protothaca staminea (Conrad, 1837)	45.7‡	9.6	Bi/INSF
Tresus sp.	6.3	0.6	Bi/INSF
Turbonilla raymondi Dall and Bartsch, 1909	6.3	1.2	Ga/VAGP
Saxidomus gigantea (Deshayes, 1839)	5.0	2.0	Bi/INSF
Nutricola sp.§	4.7	1.2	Bi/INSF
Clinocardium nuttallii (Conrad, 1837)	2.0‡	1.0	Bi/INSF
Cryptomya californica (Conrad, 1837)	0.3	0.6	Bi/INSF
Transported components			
Ostrea lurida Carpenter, 1864	53.0	—	—
Mytilus edulis Linné, 1758	20.7	—	—
Macoma nasuta (Conrad, 1837)	6.7	—	—
Odostomia nota Dall and Bartsch, 1909	6.7	—	—
Cylichnella culcitella var. *eximia* (Baird, 1863)	4.0	—	—
Brachyura indet.	2.7	—	—
Mysella tumida (Carpenter, 1864)	1.3	—	—
Mopalia sp.	0.3	—	—
Cliona sp.	rare‖	—	—
Polydora sp.	rare	—	—

* For broken mollusk specimens: apex had to be present to count as one gastropod, beak to count as ½ bivalve.

† Type organism:

Bi	bivalve mollusk
Ga	gastropod
Pp	polyplacophoran
Ci	cirriped
Ma	malacostracan
An	annelid worm
Br	bryozoan
Pr	sponge
Vt	vertebrate
Pt	plant

Substrate niche and feeding group:

EPSF	epifaunal suspension-feeder
INSF	infaunal suspension-feeder
INDF	infaunal deposit-feeder
VAGP	vagrant ectoparasite
VAGC	vagrant carnivore or macrophagous scavenger
VAGG	vagrant grazer or microphagous scavenger
PP	primary producer

‡ Some specimens may have been transported from adjacent slough-basin (see Table 2).

§ Possibly extinct.

‖ Where counts of individuals were not possible (as with shell-boring organisms) the terms common, uncommon, and rare are used.

Bluffs Sandstone; (5) lower to middle Pleistocene Carlotta Formation; and (6) middle to upper Pleistocene Hookton Formation. Depositional environments and age relationships of these units were re-evaluted by Ingle (1976), Wagner (1980), Morrison and Sarna-Wojcicki (1981), and Sarna-Wojcicki et al. (1987).

Beginning roughly 500,000 yr B.P., Humboldt Basin deposits were subjected to tectonic compression directed from the northeast and southwest. This is reflected in the series of northwest-trending folds and thrust faults that extend across coastal Humboldt County (Carver 1985; Carver et al. 1986). Hookton Formation beds accumulated for the most part in downwarped areas within marginal marine and coastal alluvial plain settings after this deformation had begun. Ogle (1953) considered the Hookton separate from the Wildcat Group owing to its stratigraphic position above a regional angular unconformity. In most outcrops the formation consists of discontinuous sand beds, sandy conglomerate, thin interbeds or lenses of mud, and at least two volcanic ash layers. Mud interbeds in the type area south of Eureka often contain an *Ostrea–Saxidomus* invertebrate fauna like the one we describe from our study site. Where it has not been disrupted by faulting, the Hookton is an

TABLE 2. FOSSILS FROM SLOUGH-BASIN MUD FACIES (SEE FIG. 3, 5).

Taxa	Average no. individuals/ liter sample* ($n = 5$)	Standard deviation	Type organism/substrate niche and feeding group†
Autochthonous components (subtidal, muddy-bottom oyster garden association)			
Ostrea lurida Carpenter, 1864	119.0	44.5	Bi/EPSF
Odostomia nota Dall & Bartsch, 1909	32.0	11.4	Ga/VAGP
Balanus sp.	25.8‡	21.7	Ci/EPSF
Protothaca staminea (Conrad, 1837)	17.8	9.9	Bi/INSF
Bittium eschrichtii (Middendorff, 1849)	13.0	12.2	Ga/VAGG?
Mysella tumida (Carpenter, 1864)	3.4	1.5	Bi/EPSF?
Macoma nasuta (Conrad, 1837)	3.2	1.1	Bi/INDF
Nutricola sp.§	2.6	4.2	Bi/INSF
Mopalia sp.	2.4	1.5	Pp/VAGG
Mytilus edulis Linné, 1758	2.0	1.2	Bi/EPSF
Granulina margaritula (Carpenter, 1857)	0.8	0.8	Ga/VAGG?
Cylichnella culcitella var. *eximia* (Baird, 1863)	0.8	0.8	Ga/VAGC
Clinocardium nuttallii (Conrad, 1837)	0.8	0.8	Bi/INSF
Alvinia compacta (Carpenter, 1864)	0.6	0.9	Ga/VAGG?
Littorina scutulata Gould, 1849	0.6	0.9	Ga/VAGG
Brachyura indet.	0.4	0.5	Ma/VAGC
Polydora sp.	common‖	—	An/INSF
Cliona sp.	uncommon	—	Pr/INSF
Spathipora sp.	uncommon	—	Br/INSF
Zosteraceae indet.	uncommon	—	Pt/PP
Fish bones	rare	—	Vt/VAGC?
Transported components			
Saxidomus gigantea (Deshayes, 1839)	0.6	—	—
Hinnites giganteus (Gray, 1825)	0.2	—	—
?*Fissurella* sp.	0.2	—	—
?*Tricolia* sp.	0.2	—	—
Turbonilla raymondi Dall & Bartsch, 1909	0.2	—	—
Clypeastroida indet.	rare	—	—
From float only			
Diodora aspera (Rathke *in* Eschscholtz, 1833)		rare, transported	
Nassarius mendicus (Gould, 1849)		rare, autochthonous?	

Superscripts and abbreviations explained in footnotes of Table 1.

essentially flat-lying unit with beds dipping <5°. A maximum age of 700,000 and minimum age of 120,000 yr B.P. have been determined for the formation based on radiometric dating of volcanic ash and amino acid racemization analysis of *Saxidomus* shells (Kennedy 1978; Meyer et al. 1980; Wagner 1980).

We review the Hookton Formation at some length because the "pre-terrace" Quaternary deposits at the mouth of Mad River were previously included in this formation by Evenson (1959). Any formation assignment in this area is problematic because of faulting, lack of continuous exposures, and a dearth of unique lithologies or conspicuous marker beds. Our locality, however, could be within the Hookton Formation because of close resemblance to Hookton lithologies; mouth of Mad River deposits are largely unconsolidated sands and sandy gravels with subordinate muddy sediments of nearshore marine to estuarine origin. This lithologic correlation is supported by a virtual lack of deformation of beds at our site, except near a major fault, and fossil associations consisting almost exclusively of extant species. An alternative interpretation was made by Carver (1985), who mapped lower to middle Pleistocene Falor Formation deposits in stream valleys along the western edge of Dows Prairie, extending the unit to the coast from its type area near Maple Creek and Korbel, inland Humboldt County (see Manning and Ogle 1950). Carver (pers. comm., June 1986) argued that: (1) the term "Hookton Formation" should be used only in its type area near

the mouth of Eel River, but it has questionable validity even there because it may not everywhere be separated from the Wildcat Group by a regional unconformity and may grade downward into upper Wildcat deposits; and (2) Hookton and Falor lithologies are identical, as far as anyone knows, and the term "Falor Formation" should be considered a senior synonym in the Mad River Fault Zone in any case. These units deserve more detailed study, and type and reference sections need to be established before firm lithostratigraphic correlations can be made.

In addition, Kohl (1974) used the informal designation "Crannell beds" for possibly coextensive Pleistocene deposits exposed near the mouth of Little River, 4 km north of our locality. Kohl's report is important for its complete checklist of fossils from the Crannell site. Roth (1979:77–79) discussed relationship of stratigraphy and fauna from this locality.

Mouth of Mad River Locality.—Sediments at our study site are mostly loose, olive brown, gravelly sands. The sand is medium to fine, moderately sorted, and subround to subangular. The only significant accumulation of silt–clay sediments is a thin, medium gray mud bed containing abundant oyster shells and plant fossils (Fig. 2, 3).

The local section begins at river level with a partially exposed unit of cross-bedded sand and gravel (Fig. 4a). Cross-stratification sets are trough- to wedge-shaped. Gravel occurs in lenticular beds, laterally continuous tabular beds, and as small channel-fill structures. Gravel beds are thicker near the bottom of the outcrop, and are normal-graded and trough cross-stratified internally. In the basal meter, rare *Ophiomorpha* burrows approximately 1 cm in diameter are located directly below a laterally continuous layer of planar-laminated, slightly muddy sand. Occasional flat lenses of peaty, silty sand also occur at this level. The assemblage of textures and structures suggests deposition in a high-energy nearshore marine setting, immediately seaward of a foreshore swash zone, which probably included the wave build-up and surf zone divisions described by Clifton et al. (1971). Thick, poorly graded gravel beds probably represent winter storm deposits, and rip currents may have formed the small gravel-filled channels (Leithold and Bourgeois 1984); cross-stratified sand and lenticular gravelly sand probably represent nearshore megaripples (Clifton et al. 1971). The laminated muddy sand and burrowed zone might indicate an interval of relatively low energy, or a slightly protected patch of seafloor buried and preserved by migrating megaripples. Abundance of cobbles and pebbles suggests proximity to a river mouth where coarse clastics were delivered directly into the ocean (David Miller, pers. comm., October 1986).

This high-energy facies grades upward into low-angle cross-stratified to planar-laminated sand. Texture of the sand fraction is similar to that of the underlying unit, but thick lenses and beds of gravel are lacking (Fig. 4b). This appears to be a strand-plain deposit formed in foreshore swash, beach platform, and overwash zones (Clifton 1969; Carter 1978; McCubbin 1982). Comparable environments can be seen in the modern strand-plain and spit complex located between the lower reaches of Mad River and the ocean (Fig. 1).

The strand-plain facies grades upward into a bed of burrow-mottled sand containing abundant bivalves usually in the upper 30–50 cm. Considering facies succession, bioturbate texture, and the presence of numerous infaunal bivalves in living positions within burrows (notably *Saxidomus* and *Tresus*), it appears that this unit was deposited in an intertidal to shallow subtidal, backbar sandflat bordering a protected slough.[1] Fossils from this facies are listed in Table 1.

Above the shelly sand, a conspicuous bed of gray mud contains slightly carbonized in situ eelgrass (Zosteraceae indet.) in the lower half and abundant *Ostrea* shells in the upper half. Blocks of this material have weathered out of the bluff face and occur at river level, in some places mixed with modern beach deposits (Fig. 4c). The mud with eelgrass fragments appears to be an intertidal to shallow subtidal mudflat deposit; the *Ostrea* bed represents oyster "gardens" that flourished in a shallow subtidal, muddy-bottom slough-basin. Fossils from the oyster-rich interval are listed in Table 2.

We did not study units above the stratigraphic level of the *Ostrea* bed. Generally, these consist

[1] We use "slough" to mean a localized coastal depression or basin protected from the open ocean by a bay-mouth bar, but smaller and shallower than most lagoons or bays; this would include abandoned river channel segments, arms of larger lagoons, small pre-existing depressions that become flooded during high stands of sea level, and other, short-lived backbar estuarine settings of limited areal extent.

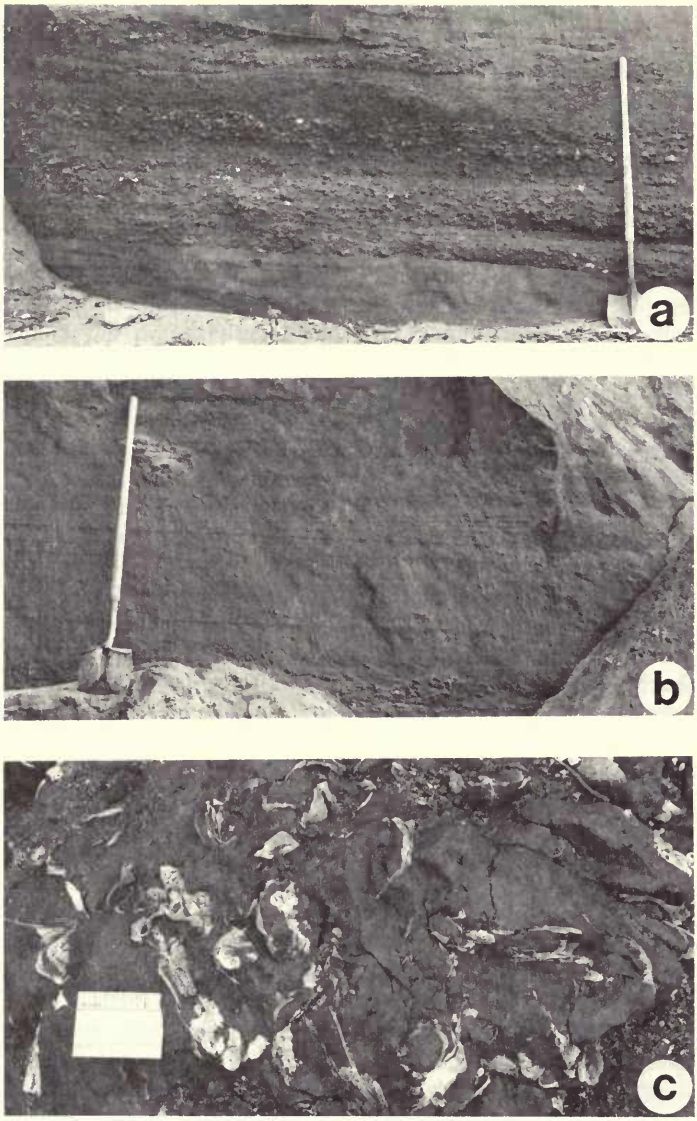


FIGURE 4. Close views of sediments and fossils: *a*, gravel beds in nearshore facies; *b*, horizontal to low-angle cross-stratified sand in strand-plain facies; *c*, boulder of slough-basin mud containing a clump of *Ostrea lurida*. Shovel in *a* and *b* is about 1.5 m long.

of pebbly sands that are covered by vegetation and slumped over subjacent beds along the bluff line.

The vertical transition from nearshore marine to backbar slough facies is a progradational sequence produced when a high-energy surf zone was replaced first by a barrier bar or spit (probably lacking extensive development of eolian deposits), and later by localized, short-lived paralic environments (see Carter 1978; Clifton 1982; McCubbin 1982). Such closely spaced, patchy, and rapidly changing depositional environments can be seen today along the coasts of northern California and Oregon, in segments between prominent rocky headlands where beaches are fully developed. In these areas of sediment accumulation, small lagoons or other types of estuarine basins with fringing marshes and sandflats are protected from the open ocean by emergent bay-mouth sand bars.

Fossil Associations

Two distinctly different fossil associations (i.e., skeletal remains derived from a single, once-living community) were identified in multiple samples: (1) an intertidal to shallow subtidal sandy-bottom association, from the slough-margin sandflat facies (Table 1); and (2) a shallow subtidal muddy-bottom oyster garden association, from the slough-basin mud facies (Table 2). These were recognized by first separating autochthonous from transported shells, and then considering the preferred habitats of living representatives of the extant species (Smith and Carlton 1975; Morris et al. 1980; Ricketts et al. 1985). Transported shells were recognized by their abraded surfaces, fragmentation, and chalky or iron-stained appearance. Species interactions, such as parasitism and commensalism, were deduced by comparison with modern benthic communities and by noting infestations of epi- and endozoans. Both associations were dominated by bivalves and gastropods from a small shallow basin located landward of a strand-plain platform.

Samples from the sandflat deposit contained abundant balanid barnacles, occurring as disarticulated side plates, which in life probably covered the exposed surfaces of dead mollusk shells awash on the sandflat. Many of the dead shells utilized by *Balanus* sp. were *Ostrea lurida* derived from the adjacent slough-basin oyster clumps. Burrowing suspension-feeding clams, however, dominated the in-place fauna in terms of preserved biovolume and species richness (six of eight species). Among these, *Saxidomus gigantea* and *Tresus* sp. were found frequently in life orientations within burrows. Others, including *Protothaca staminea,* usually occurred as disarticulated valves and fragments. Presence of the commensal bivalve *Cryptomya californica* implies the presence of large, soft-bodied infauna such as echiurid worms and anomuran shrimps (Smith and Carlton 1975:130). The only gastropod that appeared to be in place was the minute pyramidellid *Turbonilla raymondi,* an ectoparasite with an unknown but probably infaunal host. Considering parasitic life habits of this small snail, its fragile shell, and the rigors of life on the sandflat surface, *T. raymondi* probably inhabited the burrow of its host. The list of indigenous species from the sandflat deposit is short and exclusive, with many organisms that either tolerated turbulence and exposure during tidal cycles (e.g., *Balanus*), or lived protected from periodic exposure well beneath the surface in burrows (e.g., *Saxidomus, Tresus*). Presence of large numbers of slow-burrowing *Protothaca* and bioturbate fabric of the bed indicate a fairly stable substratum rather than a constantly shifting sandy bottom. The original sandflat community is reconstructed in Figure 5a.

The oyster garden association differed sharply from the sandflat fauna in being dominated numerically by epibenthic mollusks (66.7% of individuals). Preserved biovolume was concentrated in *Ostrea lurida,* which occurred in isolated clumps surrounded by slightly shelly mud matrix (Fig. 4c). The oyster shells still displayed the original reddish-brown color mottles typical of the species (Hertlein 1959). Occurring with *O. lurida* were the following ecologic associates: (1) *Balanus* sp., exploiting abundant oyster clumps as islands of hard substrata on an otherwise uninhabitable muddy seafloor; (2) another pyramidellid snail, *Odostomia nota,* a likely ectoparasite on the oysters; and (3) a commensal or parasitic polychaete worm, *Polydora* sp., living in borings or embedments in oyster valves. Intervening muddy patches between oyster clumps were inhabited by infaunal bivalves, including *Protothaca staminea,* a suspension-feeder and ubiquitous species in both fossil associations, and *Macoma nasuta,* a deposit-feeder preferring protected muddy-bottom settings. Gastropod components, in addition to *O. nota,* consisted of *Bittium eschrichtii,* diminutive *Granulina margaritula,* and a probable microcarnivore, *Cylichnella culcitella* var. *eximia*—all of which have obscure ecologic roles in marginal marine communities. In addition, the association contained rare valves of the chiton *Mopalia* sp., which probably grazed green algae or diatoms from oyster shells. The indigenous fauna of the slough-basin mud facies totals at least 21 species representing perhaps the most complete and best preserved estuarine fossil association yet reported from late Pleistocene deposits of northern California. All trophic levels are represented to some extent, including primary producers (eelgrass), primary consumers (barnacles, bivalves, some gastropods), carnivores and scavengers (some gastropods and crabs), and parasites (pyramidellid snails). The original oyster garden community is reconstructed in Figure 5b.

Faunal transition in the mouth of the Mad

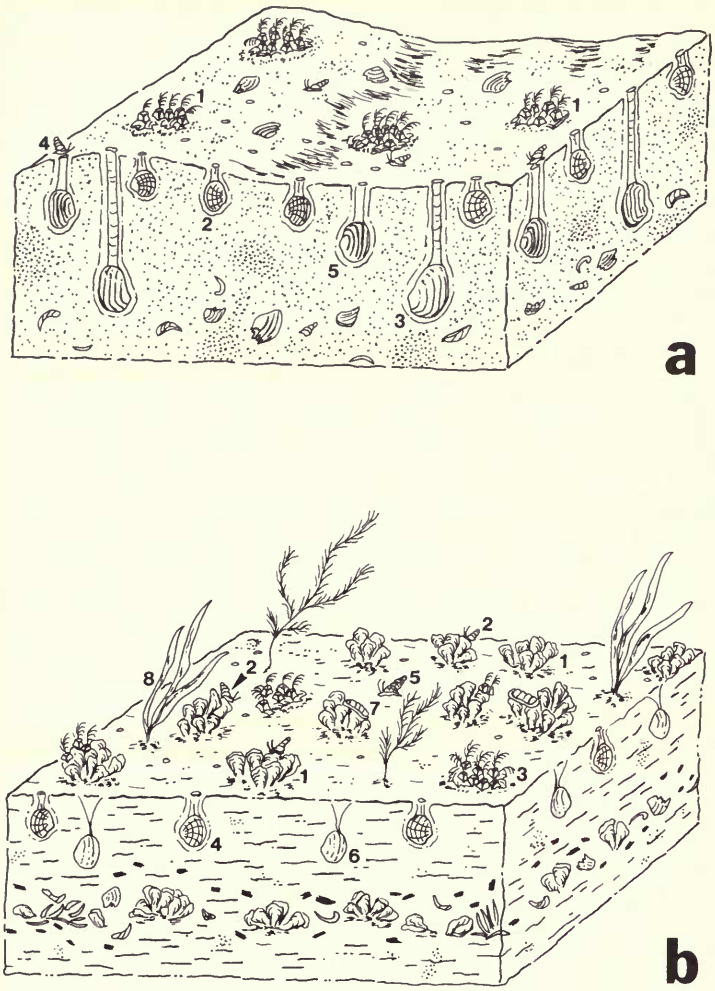


FIGURE 5. Reconstruction of benthic communities: *a*, sandflat community with (*1*) *Balanus* sp., (*2*) *Protothaca staminea*, (*3*) *Tresus* sp., (*4*) *Turbonilla raymondi*, and (*5*) *Saxidomus gigantea*; *b*, oyster garden community with (*1*) *Ostrea lurida*, (*2*) *Odostomia nota*, (*3*) *Balanus* sp., (*4*) *Protothaca staminea*, (*5*) *Bittium eschrichtii*, (*6*) *Macoma nasuta*, (*7*) *Mopalia* sp., and (*8*) eelgrass.

River section was the result of community replacement involving habitat alteration and species turnover (Miller 1986). This resulted when muddy sediments prograded over sandflat areas either as the slough-basin deepened and expanded in area or as protection from the open ocean became more complete at our site. Organisms responded to changes in substrate (from sand to mud), to reduced water turbulence and tidal exposure, and probably to changes in salinity fluctuations (Ricketts et al. 1985). The two original communities must have been situated adjacent to each other because large numbers of transported oyster valves were mixed with the sandflat fauna (Table 1) and the transition occurs within a thin (<1 m), continuous stratigraphic interval.

ACKNOWLEDGMENTS

We thank Raymond Burke, Gary Carver, and David Miller for background information on regional tectonics and sedimentology of our study site, and for comments on an earlier version of this paper. We also thank four anonymous reviewers for thorough evaluations that improved the quality of the final version. Frank Bernard

helped us with identification of *Nutricola*. Nancy Walters processed bulk samples, Laura Leitch assisted with field work, and Camellia Armstrong and Carolyn Young typed drafts of the manuscript. Manuscript preparation was funded in part by Humboldt State University Foundation.

Literature Cited

Abbott, R. T. 1974. American seashells, 2nd ed. Van Nostrand Reinhold Co., New York. 663 pp.

Bernard, F. R. 1982. *Nutricola* n. gen. for *Transennella tantilla* (Gould) from the northeastern Pacific (Bivalvia: Veneridae). Venus 41:146–149.

Carter, C. H. 1978. A regressive barrier and barrier-protected deposit: depositional environments and geographic setting of the Late Tertiary Cohansey Sand. Jour. Sed. Petrol. 48:933–950.

Carver, G. A. 1985. Quaternary tectonics north of the Mendocino Triple Junction: the Mad River Fault Zone. Pp. 155–167 *in* Redwood Country. M. E. Savina, ed. American Geomorphological Field Group Field Trip Guidebook.

Carver, G. A., R. M. Burke, and H. M. Kelsey. 1986. Deformation of late Pleistocene marine terraces along the California coast north of Cape Mendocino. Geol. Soc. Am., Abstracts with Programs 18:93.

Clifton, N. E. 1969. Beach lamination—nature and origin. Marine Geol. 7:553–559.

———. 1982. Estuarine deposits. Pp. 179–189 *in* Sandstone depositional environments. P. A. Scholle and D. Spearing, eds. Am. Assoc. Petrol. Geol., Tulsa, Oklahoma.

Clifton, H. E., R. E. Hunter, and R. L. Phillips. 1971. Depositional structures and processes in the non-barred high-energy nearshore. Jour. Sed. Petrol. 41:651–670.

Dall, W. H. and P. Bartsch. 1909. A monograph of West American pyramidellid mollusks. U.S. Natl. Mus. Bull. 68. 258 pp. + 30 pl.

Evenson, R. E. 1959. Geology and ground-water features of the Eureka area, Humboldt County, California. Water-Supply Paper 1470, U.S. Geol. Survey. 80 pp.

Fitch, J. E. 1953. Common marine bivalves of California. Fish Bull. No. 90, California Dept. Fish and Game. 102 pp.

Griffith, L. M. 1975. The intertidal univalves of British Columbia. Handbook 26, British Columbia Prov. Mus., Victoria. 101 pp.

Hertlein, L. G. 1959. Notes on California oysters. Veliger 2:5–10.

Hopps, T. and E. Horan. 1983. Subsurface stratigraphy: Eel River basin. Pp. 1–28 *in* Selected papers of the Pacific Section 1983 annual meeting, Sacramento, California. R. L. Hester and D. E. Hollinger, eds. Pacific Section, Am. Assoc. Petrol. Geol., Los Angeles, California.

Hoskins, E. G. and J. R. Griffiths. 1971. Hydrocarbon potential of northern and central California offshore. Am. Assoc. Petrol. Geol. Memoir 15, 1:212–228.

Ingle, J. C., Jr. 1976. Late Neogene paleobathymetry and paleoenvironments of Humboldt Basin, northern California. Pp. 53–81 *in* The Neogene symposium. H. Ter Best and W. W. Wornardt, eds. Pacific Section, Soc. Econ. Paleont. Mineral. San Francisco, California.

Keen, A. M. and E. Coan. 1974. Marine molluscan genera of western North America, 2nd ed. Stanford Univ. Press, Stanford, California. 208 pp.

Kennedy, G. L. 1978. Pleistocene paleoecology, zoogeography, and geochronology of marine invertebrate faunas of the Pacific northern coast. Ph.D. Dissertation, Univ. California, Davis. 824 pp.

Kohl, R. F. 1974. A new late Pleistocene fauna from Humboldt County, California. Veliger 17:21–219.

Leithold, E. L. and J. Bourgeois. 1984. Characteristics of coarse-grained sequences deposited in nearshore, wave-dominated environments—examples from the Miocene of south-west Oregon. Sedimentology 31:749–775.

Manning, G. A. and B. A. Ogle. 1950. Geology of the Blue Lake Quadrangle, California. California Div. Mines and Geol. Bull. 148. 35 pp.

McCubbin, D. G. 1982. Barrier-island and strand-plain facies. Pp. 247–279 *in* Sandstone depositional environments. P. A. Scholle and D. Spearing, eds. Am. Assoc. Petrol. Geol., Tulsa, Oklahoma.

Meyer, C. E., M. J. Woodward, A. M. Sarna-Wojcicki, and C. W. Naeser. 1980. Zircon fission track dating of 0.45 million years on ash in the type section of the Merced Formation, west central California. Open File Report 80-701, U.S. Geol. Surv. 9 pp.

Miller, W., III. 1986. Paleoecology of benthic community replacement. Lethaia 19:225–231.

Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980. Intertidal invertebrates of California. Stanford Univ. Press, Stanford, California. 690 pp.

Morrison, S. and A. Sarna-Wojcicki. 1981. Time equivalent bay and outer shelf faunas of the Neogene Humboldt Basin, California and correlation to the North Pacific microfossil zones of DSDP 173. Pp. 130–131 *in* Proceedings of IGCP-114 international workshop on Pacific Neogene biostratigraphy. Osaka Museum Nat. Hist., Osaka, Japan.

Ogle, B. A. 1953. Geology of the Eel River Valley area, Humboldt County, California. California Div. Mines and Geol. Bull. 164. 128 pp.

Oldroyd, I. S. 1927. The marine shells of the west coast of North America, Vol. II. Stanford Univ. Press, Stanford, California. 941 pp. + 108 pl.

Ricketts, E. F., J. Calvin, J. W. Hedgpeth, and D. W. Phillips. 1985. Between Pacific tides, 5th ed. Stanford Univ. Press, Stanford, California. 652 pp.

Roth, B. 1979. Late Cenozoic marine invertebrates from northwest California and southwest Oregon. Ph.D. Dissertation, Univ. California, Berkeley. 803 pp.

Sarna-Wojcicki, A. M., S. D. Morrison, C. E. Meyer, and J. W. Hillhouse. 1987. Correlation of Upper Cenozoic tephra layers between sediments of the western United States and eastern Pacific Ocean and comparison with biostratigraphic and magnetostratigraphic age data. Geol. Soc. Am. Bull. 98:207–223.

Smith, R. I. and J. T. Carlton, eds. 1975. Light's manual: intertidal invertebrates of the central California coast, 3rd ed. Univ. California Press, Berkeley. 716 pp.

Wagner, J. R. 1980. Summary of regional stratigraphy and geologic structure. Pp. A1–A73 *in* Evaluation of the potential for resolving the geologic and seismic issues at the Humboldt Bay Power Plant unit no. 3, prepared for the Pacific Gas and Electric Company. Unpubl. report, Woodward-Clyde Consultants, San Francisco, California.

Willett, G. 1928. Notes on some Pacific Coast acteocinas, with description of one new subspecies. Nautilus 42:37–38.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 11, pp. 267-276, 8 figs. April 12, 1988

STUDIES ON THE ZOARCIDAE (TELEOSTEI: PERCIFORMES) OF THE SOUTHERN HEMISPHERE. II. TWO NEW GENERA AND A NEW SPECIES FROM TEMPERATE SOUTH AMERICA

By

M. Eric Anderson

Department of Ichthyology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

ABSTRACT: Comparative osteological studies of two South American zoarcid fishes revealed both to be distinctive, primitive lycenchelyines, as defined by Anderson (1984). *Maynea microphthalma* (Norman, 1937) and *Letholycus magellanicus* sp. nov., comprise the new genus *Letholycus,* distinguished by reduction of its chain of suborbital bones, gill slit, palatal arch, pectoral fin, vertebral number, and pelvic fin loss. *Ophthalmolycus stehmanni* Gosztonyi, 1977, comprises the new, monotypic genus *Plesienchelys,* distinguished by its anteriorly broadened pterotic bones, open preoperculomandibular canal, uniquely tapering tail, and few vertebrae. Both genera are endemic to the upper continental slope off Argentina.

RESUMEN: Estudios osteólogicos comparativos de dos especies de peces zoarcidos de Sur America revelan que ambos han de ser distintivos de tipos primitivos lycenchelyinos de Anderson (1984). *Maynea microphthalma* (Norman, 1937) y *Letholycus magellanicus* sp. nov., comprende el género *Letholycus,* distinguido por su redocido cadena de huesos suborbitales, abertura branquial, arco paladial, aleta pectoral, numera de vertebras, y la perdida de la aleta pelvica. *Ophthalmolycus stehmanni* Gosztonyi, 1977 comprende un tipo único en el género *Plesienchelys,* distinguido por sus anchos huesos pteróticos, canal preoperculomandibular abierta, cola de terminación angular única, y pocas vertebras. Los dos géneros son endemicos a la parte alta de la pendiente continental de las costas argentinas.

Received May 20, 1987. Accepted August 19, 1987.

INTRODUCTION

In his review of temperate South American Zoarcidae, the first since Norman (1937), Gosztonyi (1977) added three new genera and five new species to this fauna for a total of 20 species. The addition of three distinctive genera indicated that the zoarcid fauna of this area (Magellan Province of Briggs 1974) may be more speciose than previously thought. Gosztonyi's new material came from littoral collections made by himself and colleagues, and from exploratory fishing operations of the Federal Republic of Germany's Institut für Seefischerei, Hamburg (ISH).

I have recently studied the ISH collections, including material obtained since 1977. My studies have been greatly enhanced by previously unreported collections of the U.S. Antarctic Research Program from the Magellan Province housed at the Los Angeles County Museum of Natural History (LACM) as well as material collected by Soviet colleagues housed at the Zoological Institute in Leningrad (ZIL). I have reported on these collections from Antarctica elsewhere (Anderson, in press).

Norman (1937) described *Melanostigma microphthalmus* from the 1928 WILLIAM SCORESBY collections off the Falkland Islands.

The species was placed in *Maynea* Cunningham, 1871, by McAllister and Rees (1964) and Gosztonyi (1977), but the anatomy of this rare form was unknown to these authors. The new ISH collections include a specimen that I was able to dissect and partially clear and stain, revealing its distinctive, reduced skeleton. Two other specimens were found, at first identified as *M. microphthalmus,* but on closer inspection were discovered to be a second, closely related species. Both forms comprise the new genus *Letholycus* described here and contrasted with *Maynea,* recently redescribed (Anderson, 1988).

Gosztonyi (1977) described *Ophthalmolycus stehmanni* from a single specimen taken during the 1971 WALTHER HERWIG cruise north of the Falkland Islands. Although Gosztonyi was able to compare his specimen with the then only known specimen of the type species of *Ophthalmolycus* Regan, 1913 (*Lycodes macrops* Günther, 1880), the osteology of these two forms remained unknown. I have examined six additional specimens each of *O. macrops* and *O. stehmanni* from the ISH and LACM collections, and made osteological observations on each species. As a result, the new genus *Plesienchelys* is herein erected for *O. stehmanni.*

Methods and Materials

Measurements were made with ocular micrometer or dial calipers to the nearest 0.1 mm. Osteological observations were made on cleared and stained specimens (Dingerkus and Uhler 1977) and drawings made with the aid of a camera lucida. Definitions of characters and measurements follow those of Gosztonyi (1977) and Anderson (1982, 1984), repeated in the first part of this series (Anderson, in press). Character state modifiers are based on those numerically scored characters of Anderson (1984). Museum abbreviations follow Leviton et al. (1985).

Abbreviations for bone names used in the text figures are as follows:

act—actinosts
ang—anguloarticular
basbr—basibranchial
br—branchiostegal ray
cerbr—ceratobranchial
cerhy—ceratohyal
cl—cleithrum
cor—coracoid
ect—ectopterygoid
epibr—epibranchial
epihy—epihyal
ex—lateral extrascapular
exoc—exoccipital
fr—frontal
hyom—hyomandibula
hypbr—hypobranchials
hyphy—hypohyal
i2–4—infrapharyngobranchials
inthy—interhyal
lat eth—lateral ethmoid
max—maxilla
mep—mesopterygoid
mes—mesethmoid
pal—palatine
pas—parasphenoid
pcl—postcleithrum
pel—pelvic (basipterygium)
pop—preopercle
ptem—posttemporal
pto—pterotic
pts—pterosphenoid
quad—quadrate
scap—scapula
soc—supraoccipital
sph—sphenotic
supcl—supracleithrum
urohy—urohyal

Plesienchelys gen. nov.

Type Species.—*Ophthalmolycus stehmanni* Gosztonyi, 1977.

Diagnosis.—A lycencnelyine zoarcid as defined by Anderson (1984) with body slender, tail relatively elongate; anterior portion of pterotic bones wider than posterior portion; preoperculomandibular canal passing through trough in preopercle and dentary; palatal arch well developed, with ectopterygoid and mesopterygoid overlapping more than half anterior and dorsal surfaces of quadrate; vertebrae 19–21 + 66–73 = 86–93; tail sharply tapering posteriorly; pyloric caeca absent. Other characters those of single species.

Etymology.—From the Greek πλείων, majority (used as primitive in zoology), and 'ενχελυς, eel; combination refers to this taxon's many primitive characters. Gender: feminine.

Plesienchelys stehmanni (Gosztonyi, 1977)

(Fig. 1A, 2, 3, 4A, 5A, 6A)

Ophthalmolycus stehmanni Gosztonyi, 1977:230–233, fig. 16, 17.

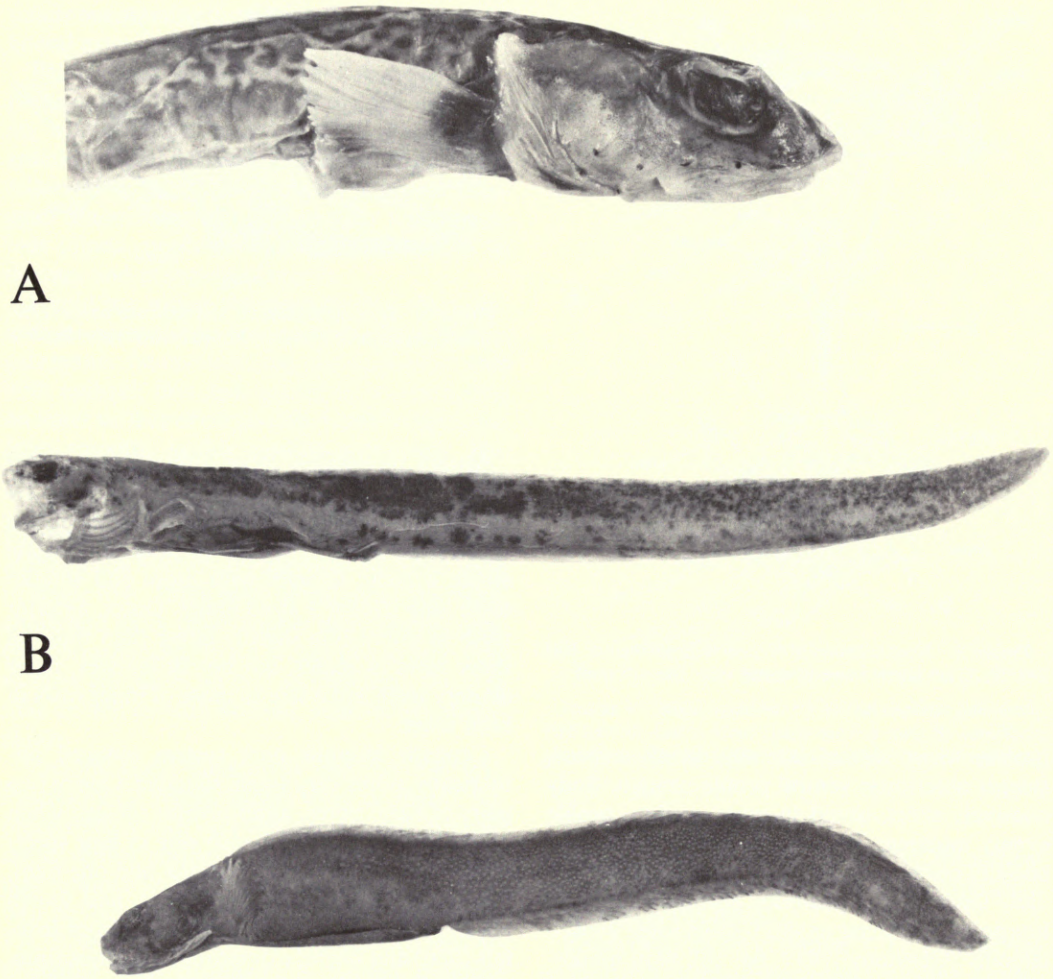


FIGURE 1. Lateral views of: A) *Plesienchelys stehmanni,* head and trunk, ISH 377/78, 204 mm; B) *Letholycus microphthalmus,* ISH 376/78, 90 mm; C) *Letholycus magellanicus,* holotype, ISH 164/78, 147 mm.

MATERIAL EXAMINED.—ISH 317/71 (holotype; 165 mm SL); north of Falkland Isls. (49°13′S, 58°45′W); FFS WALTHER HERWIG (WH) sta. 294/71; 485–506 m; 14 Feb. 1971. ISH 249/78 (1; 193 mm, cleared and stained); north of Falkland Isls. (49°30.7′S, 57°34.8′W); WH sta. 634/71; 340–345 m; 13 June 1978. ISH 377/78 (1; 202 mm); Argentine slope (40°15.9′S, 56°07.7′W); WH sta. 719/78; 975 m; 21 July 1978. ISH 383/71 (1; 247 mm); south of Falkland Isls. (52°57.0′S, 58°30.2′W); WH sta. 825/78; 465 m; 20 Aug. 1978. ISH 392/78 (1; 216 mm); off Rio de la Plata (37°33.2′S, 54°25.2′W); WH sta. 928/78; 847 m; 28 Sept. 1978. ISH 393/78 (1; 205 mm); Argentine slope (47°51.5′S, 59°33.0′W); WH sta. 982/78; 840 m; 9 Oct. 1978. LACM 10449-2 (1; 232 mm); east of Falkland Isls. (51°58′S, 56°38′W); ELTANIN sta. 558; 646–845 m; 14 Mar. 1963.

COUNTS AND MEASUREMENTS.—Vertebrae 19–21 + 66–73 = 86–93; D 80–86; A 68–77; C 9–10; P1 17–19; P2 three; vomerine teeth three to eight; palatine teeth three to seven; gill rakers 1–3 + 7–9 = 8–11; branchiostegal rays six; pseudobranch filaments one to five; pyloric caeca absent. Following measurements in percent SL: head length 15.9–17.6; pectoral fin length 8.0–9.8; predorsal length 20.6–21.8; preanal length 31.7–35.2; body height 5.1–6.6; caudal fin length 2.4–5.4. Following measurements in percent HL: head width 47.9–58.4; upper jaw length 44.1–56.4; pectoral fin length 46.2–53.6; pelvic fin length 13.3–18.4; snout length 21.1–27.3; eye diameter 28.9–37.3; gill slit length 35.7–42.9; interorbital width 6.9–8.8. Pectoral base/length ratio 47.1–58.9.

DIAGNOSIS.—As for genus.

DESCRIPTION.—Head relatively large; dorsal

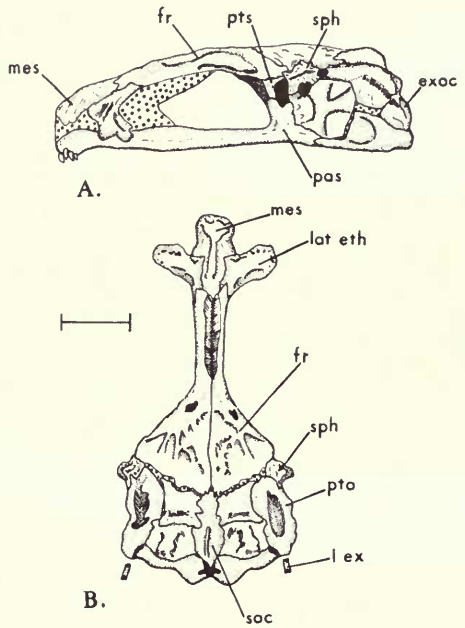


FIGURE 2. Neurocranium of *Plesienchelys stehmanni,* ISH 249/78: A) left lateral view; B) dorsal view. Bar = 5 mm.

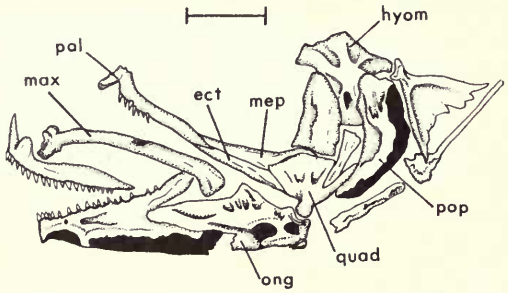


FIGURE 3. Jaws, suspensorium, and opercular bones of *Plesienchelys stehmanni,* ISH 249/78, left lateral view. Bar = 5 mm.

profile, when viewed laterally, gently curved, steeper anteriorly; ventral profile straight. Body relatively short, ovoid in cross section, profile evenly tapering. Tail laterally compressed, especially posteriorly; anterior region of tail gradually tapering, but posterior portion thinned to fine point, appearing as sharp spike when viewed laterally (Gosztonyi 1977, fig. 16). Skin moderately firm, thin, with subdermal gelatinous layer covering head and body, this not present on tail. Body lateral line with mediolateral branch running to middle of tail and ventrolateral branch running to tail tip. Scales minute, cycloid, imbedded, extending anteriorly on tail to about one head length or less posterior to anus, formed into wedge-shaped pattern anteriorly; very few scales extend onto bases of dorsal and anal fins. Eye relatively large, ovoid, comparatively larger in smaller specimens. Gill opening nearly vertical dorsally, extending ventrally to near pelvic base; no siphonal fold formed at dorsal margin. Single pair of nostrils at snout tip, nasal tube minute, not reaching upper lip. Posterior margin of pectoral fin evenly rounded, relatively large, origin just below body midline, insertion on ventral surface of abdomen; ventralmost seven to eight rays thickened, excised at tips.

Mouth moderately large, subterminal; upper jaw 49.1–56.4% HL in adult males, 44.1–47.1% HL in adult females (no young juveniles of this species are known). Teeth in jaws and palate small, conical; females with more and smaller teeth than similarly sized males. Outer, anterior teeth in premaxilla slightly larger than those of inner rows in males, but not in females; outer dentary teeth same size as those of inner rows in both sexes.

Cephalic lateralis pore system reduced numerically, pores very small, rounded. One or two pairs of nasal pores, anteriormost present when only one (single pair on each side in four specimens, two pair in two specimens, and one right, two left pores in one). First, third, and fourth postorbital pores present, emanating from frontals (first) and lateral extrascapulars. Interorbital and occipital (supratemporal) pores absent, no supratemporal commissure across parietals. Preoperculomandibular canal with four dentary, one anguloarticular, and three preopercular pores. Seven suborbital bones in L-shaped pattern below and behind eye, with six pores emanating from ventral branch and none from ascending branch.

Parasphenoid wing low, with short posterior ramus, not reaching mid-height of trigeminofacialis foramen; frontal and parasphenoid not separated by pterosphenoid (Fig. 2A). Ethmoid cartilage extensive, protruding well into orbital fenestra. Sphenotic and parietal separated by pterotic and frontal. Anterior portion of pterotic wider than posterior portion, unlike other zoarcids, overlapping parietal somewhat (Fig. 2B). Supraoccipital moderate, narrowly contacting exoccipital posteriorly, with low mesial crest. Pa-

rietals not meeting in midline. Single, very small lateral extrascapular.

Palatal (pterygoid) arch well developed, ectopterygoid and mesopterygoid broadly articulating with quadrate, covering more than half its anterior dorsal surfaces (Fig. 3). Metapterygoid relatively large. Hyomandibular rami not elongate. Mandibular and preopercular lateralis canals joined, pores emanating from troughs in dentary and preopercle (Fig. 3).

Hyoid bar somewhat elongate (Fig. 4A). Ceratohyal–epihyal juncture smooth. Branchiostegal rays six: four articulating with ceratohyal, two with epihyal; first and second rays articulating on inner surface of ceratohyal. Urohyal thin, surfaces smooth, weakly ossified posteriorly. Hypohyals well ossified, dorsalmost reduced in size.

Branchial basket relatively well ossified; fourth basibranchial a cartilaginous pad (Fig. 5A). Ceratobranchial five (lower pharyngeal) dentate, teeth in single row. Three pairs of infrapharyngobranchials and tooth plates (upper pharyngeals) present, corresponding to gill arches two to four. One to three gill rakers on first epibranchial, seven to nine on first ceratobranchial, none on hypobranchials.

Pectoral girdle moderately reduced (Fig. 6A). Posttemporal ventral ramus weak or absent. Supracleithrum with very weak posteriorly directed dorsal ramus, and no cartilaginous lamina. Scapular foramen enclosed; scapular posterior ramus well developed. Four actinosts present bearing 17–19 pectoral fin rays; dorsalmost two rays articulating with cartilaginous lamina opposite scapular ramus. Three pelvic fin rays, distalmost about half as long as other two. Postcleithrum a reduced, curved splint.

Epipleural ribs on vertebrae 1–17. Pleural ribs on fourth to ultimate precaudal vertebrae. Dorsal

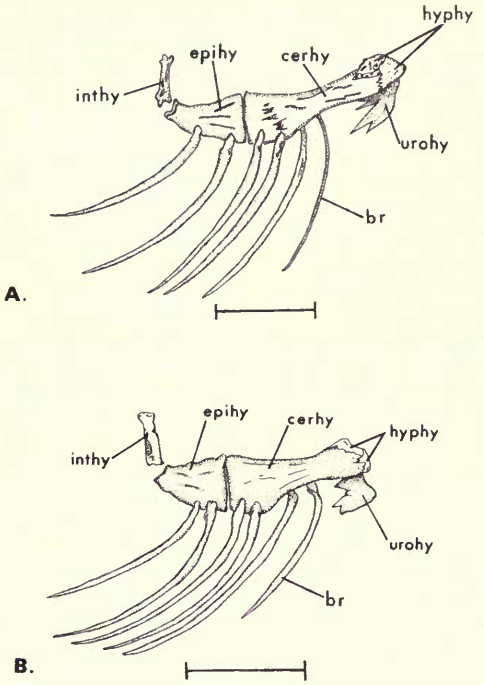


FIGURE 4. Right hyoid bar of: A) *Plesienchelys stehmanni,* ISH 249/78, lateral view; space bar = 3 mm; B) *Letholycus microphthalmus,* ISH 376/78, lateral view; bar = 2 mm.

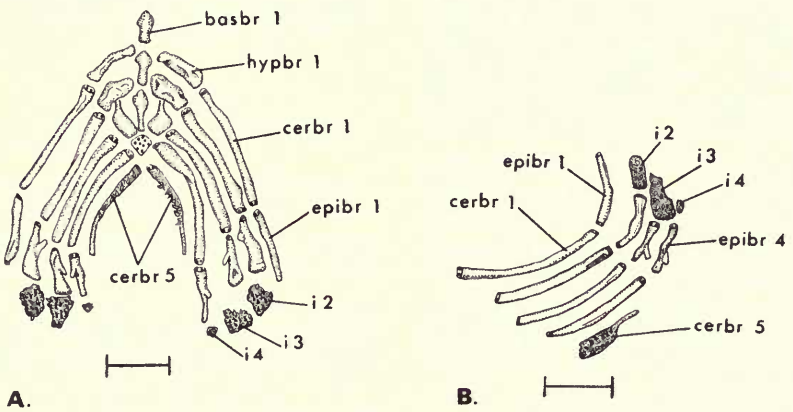


FIGURE 5. Gill arch bones of: A) *Plesienchelys stehmanni,* ISH 249/78, dorsal view, epibranchials and upper pharyngeals pulled 180° posterior to position in vivo; bar = 3 mm; B) *Letholycus microphthalmus,* ISH 376/78, anteromesial view of right elements, epibranchials and upper pharyngeals pulled 90° posterior to position in vivo; bar = 2 mm.

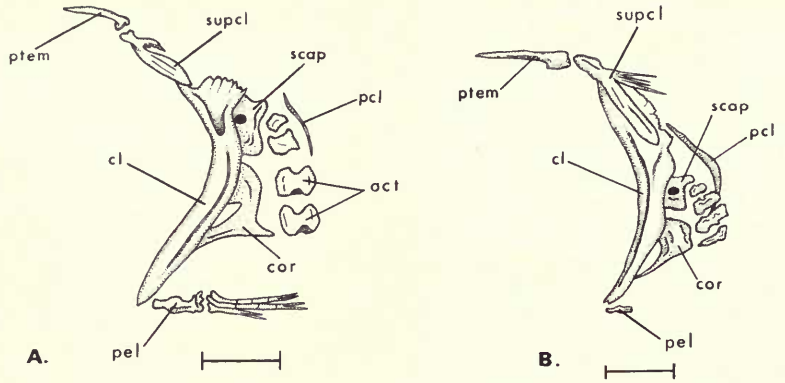


FIGURE 6. Left pectoral girdle of: A) *Plesienchelys stehmanni,* ISH 249/78, lateral view; space bar = 3 mm; B) *Letholycus microphthalmus,* ISH 249/78, lateral view; bar = 2 mm.

fin origin associated with vertebrae six to eight, with no free pterygiophores. All dorsal fin elements soft rays; first bilaterally divided near base, although unsegmented and unbranched. Last dorsal ray associated with fourth preural vertebra. Anal fin origin associated with last precaudal vertebra, with four to five ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. All anal fin elements soft rays (all segmented); last anal ray associated with second preural vertebra. Caudal fin rays nine to ten, with two epural, four upper hypural, and three to four lower hypural rays.

Palatine membrane (oral valve) weak, not reaching anterior margin of vomer. Pseudobranch filaments one to five (usually three to four), relatively short. Pyloric caeca absent.

Dorsal part of head uniformly chocolate brown; dorsal part of trunk with brown mottling extending to body midline. Flesh dull white ventrally including head. Posterior caudal region uniformly brown dorsally, uniformly dull white below. Abdomen and eye dark blue. Lining of orobranchial chamber pale.

REMARKS.—Anderson (1984) characterized *Plesienchelys stehmanni* as the primitive sister taxon to all other lycenchelyine eelpouts. These fishes, comprising 11 genera and about 70 species, are separable from all other eelpouts by two important, correlated characters: a great slenderization of the body and an elongation of the tail. In all lycenchelyines except *Plesienchelys,* the tail does not sharply taper posteriad; its height is about the same at two-thirds its length posteriorly as at the anal fin origin. In *Plesienchelys,* the shape of the tail is unique: it rapidly and evenly tapers to its tip, giving specimens the appearance of a marlin spike. The more specialized lycenchelyines are also characterized by a vertebral increase (chiefly caudal vertebrae, further elongating the tail), a head pore enlargement (with some reversal in this character), and a palatal arch reduction with the endopterygoid and mesopterygoid not overlapping half the anterior and dorsal surfaces of the quadrate. *Plesienchelys* has retained the plesiomorphic states of all these characters in having relatively few vertebrae, very small pores, and a strongly ossified palatal arch. Despite the large number of plesiomorphic states in most bone systems, the new genus is characterized by two autapomorphies: the sharply attenuated tail and the anteriorly expanded pterotic bones (Fig. 2B). The genus further differs from *Ophthalmolycus* Regan, 1913, by its troughlike passage of the preoperculomandibular canal through the dentary and preopercle.

Letholycus gen. nov.

TYPE SPECIES.—*Melanostigma microphthalmus* Norman, 1937.

DIAGNOSIS.—A lycenchelyine zoarcid as defined by Anderson (1984) with body slender, tail relatively elongate; suborbital bones four to five; gill slit above pectoral fin base, or extending ventrally to mid-pectoral base; palatal arch reduced, with ectopterygoid and mesopterygoid not overlapping half anterior and dorsal surfaces of quadrate; vertebrae 24–27 + 67–75 = 93–101; pelvic fins absent; pectoral fin rays 9–14.

ETYMOLOGY.—From the Greek λήθη, a forgetting, and λύκώδης, wolflike (after *Lycodes*), a commonly used suffix for southern

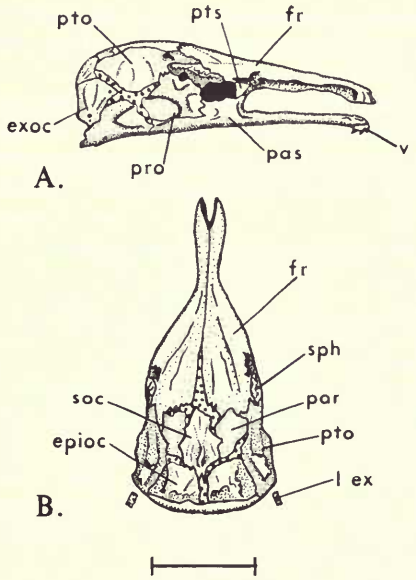


FIGURE 7. Neurocranium of *Letholycus microphthalmus*, ISH 376/78, partially reconstructed, ethmoid region removed: A) right lateral view; B) dorsal view, left side reconstructed. Bar = 2 mm.

hemisphere eelpout genera (*Ophthalmolycus, Austrolycus,* etc.). Named in reference to the distinctive, yet previously unobserved, anatomy of the species. Gender: masculine.

REMARKS.—The two species comprising the new genus differ from *Maynea* Cunningham in having only four to five suborbital bones (six in *Maynea*), normal hyomandibular rami (posterior ramus elongate in *Maynea* and relatives), smooth ceratohyal–epihyal juncture (bone interdigitating at juncture in *Maynea* and relatives), parietals not meeting in the midline (meeting in *Maynea*), and six branchiostegal rays (five in *Maynea*; Anderson, 1988: fig. 1–3).

Letholycus microphthalmus (Norman, 1937)

(Fig. 1B, 4B, 5B, 6B, 7, 8)

Melanostigma microphthalmus Norman, 1937:110, fig. 58.
Maynea microphthalmus (Norman). McAllister and Rees, 1964: 106–107, app.
Maynea microphthalma (Norman). Gosztonyi, 1977:223–224, fig. 12.

MATERIAL EXAMINED.—BMNH 1936.8.26:1047 (holotype; 83 mm SL); south of Falkland Isls. (52°40′S, 58°30′W), WILLIAM SCORESBY (WS) sta. 248; 210–242 m; 20 July 1928. BMNH 1936.8.26: 1046 (paratype; 69 mm); south of Falkland Isls. (52°25′S, 61°00′W); WS sta. 246, 267–208 m; 19 July 1928. ISH 376/78 (1; 90 mm, head partially cleared and stained); Argentine slope (45°59.3′S, 59°57.1′W); WALTHER HERWIG sta. 531/78; 580 m; 15 May 1978. LACM 10062-1 (1; 45 mm); off Cape Horn (55°47′S, 66°17′W); ELTANIN sta. 219; 115 m; 23 Sept. 1962. ZIL 39894 (1; 42 mm); Argentine slope (45°16′S, 54°54′W); OB' sta. 479; 680 m; 16 June 1978. ZIL 43285 (1; 56 mm); Argentine slope (47°17′S, 59°54′W); ZUND sta. 128; 750 m; 18 May 1974. ZIL 41568 (12; 38.5–75 mm); east of Falkland Isls. (51°57′S, 57°37′W); AKAD. KURCHATOV sta. 930; 401 m; 18 Dec. 1971.

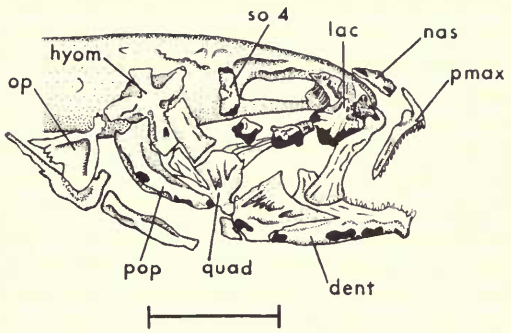


FIGURE 8. Jaws, suspensorium, opercular, and suborbital bones of *Letholycus microphthalmus*, ISH 376/78, right lateral view. Bar = 3 mm.

COUNTS AND MEASUREMENTS.—Vertebrae 24–27 + 67–77 = 94–101; D 91–96; A 69–79; C 6–8; P1 9–10; P2 absent; vomerine teeth two to five; palatine teeth 6–12; gill rakers 1–2 + 7–9 = 8–11; branchiostegal rays six (seven); pseupdobranch filaments two; pyloric caeca two. Following measurements in percent SL: head length 12.7–18.4; head width 5.8–7.2; pectoral fin length 3.8–7.2; predorsal length 15.6–18.7; preanal length 37.0–43.6; body height 6.5–7.6; caudal fin length 1.5–2.4. Following measurements in percent HL: head width 35.9–47.4; upper jaw length 29.6–36.5; pectoral fin length 29.8–52.1; snout length 17.5–26.3; eye diameter 18.4–26.0; gill slit length 15.8–17.6; interorbital width 9.9–12.5. Pectoral base/length ratio 29.4–35.9.

DIAGNOSIS.—Preoperculomandibular pores six to seven; suborbital pores four to five; postorbital pores two; occipital pore absent; pectoral fin rays 9–10; dorsal fin origin associated with vertebrae four to five; body lateral line mediolateral, extending posteriorly to just behind vertical through anal fin origin; gill opening above pectoral base; pectoral base/length ratio 29.4–35.9.

DESCRIPTION.—Head relatively short, bluntly rounded anteriorly; ventral profile very gently curved. Body relatively short, ovoid in cross section; profile not tapering posteriorly. Tail laterally compressed, especially posteriorly; anterior region of tail not tapering. Skin moderately firm, thin, with slight, subdermal gelatinous layer about abdomen. Lateral line mediolateral, neuromasts traced in two specimens along body to less than half head length posterior to vertical through anal fin origin. Scales minute, cycloid, imbedded, extending anteriorly on tail to vertical through first

third of its length; scales scattered anteriorly, not forming wedge-shaped pattern; no scales on vertical fins. Young juvenile (LACM 10062-1) without scales. Eye relatively small, rounded. Gill opening vertical ventrally, without posteriorly directed flap or siphonal fold; entirely above pectoral base. Single pair of nostrils at snout tip, nasal tube extremely long, overlapping and extending beyond upper lip to terminate about middle of lower lip (Norman 1937, fig. 58). Pectoral fin evenly rounded posteriorly, relatively small, origin well below body midline, insertion on ventral surface of abdomen; all rays excised at tips, ventralmost more so than dorsalmost; ventral rays thickened. Pectoral fin of 45-mm juvenile (LACM 10062-1) incompletely developed: its length 29.8% HL (44.8–52.1% HL in others); only four rays formed (others with 9–10 rays).

Mouth relatively small, terminal; sexual dimorphism in upper jaw lengths not detected due to small sample size ($n = 18$). Teeth in jaws and palate small, conical, in single row in dentary and premaxilla.

Cephalic lateralis pore system reduced numerically, pores enlarged. Two pair of nasal pores, located just anteromesial and posteromesial to nasal tube. First and fourth postorbital pores present, emanating from frontals (first) and lateral extrascapulars (fourth). Interorbital and occipital (supratemporal) pores absent, no supratemporal commissure across parietals. Preoperculomandibular canal with three (four in ISH 376/78) dentary, one anguloarticular, and two (ventral and middle) preopercular pores. Four (five in ISH 376/78) suborbital pores emanating from or between two or three of the four suborbital bones.

Parasphenoid wing wide, entirely below trigeminofacialis foramen; frontal and parasphenoid not separated by pterosphenoid (Fig. 7A). Sphenotic and parietal separated by frontal and pterotic (Fig. 7B). Pterotic broadest at midlength, anteriorly containing tubular passage of postorbital canal; this exits posteriorly through raised tube on surface of bone. Supraoccipital relatively large, separated from exoccipital by epioccipitals, with very low, mesial crest. Parietals not meeting in midline. Single, very small, lateral extrascapular.

Palatal (pterygoid) arch weak, ectopterygoid and mesopterygoid contacting less than half dorsal and anterior surfaces of quadrate (Fig. 8). Metapterygoid relatively large. Hyomandibula rami not elongate. Mandibular and preopercular lateralis canals joined.

Hyoid bar well ossified, not elongate (Fig. 4B). Ceratohyal–epihyal juncture smooth. Branchiostegal rays six: four articulating with ceratohyal (LACM 10062-1 with four on one side, five on the other), two with epihyal; first and second rays articulating on ventral edge of ceratohyal. Urohyal thin, surfaces smooth, weakly ossified posteriorly, anterior edge bowed forward. Hypohyals well ossified, neither reduced in size.

Branchial basket well ossified; fourth basibranchial a cartilaginous pad. Ceratobranchial five (lower pharyngeals) dentate, teeth in two irregular rows (Fig. 5B). Three pair of infrapharyngobranchials and tooth plates (upper pharyngeals) present. One or two gill rakers on first epibranchial, seven to nine on first ceratobranchial, none on hypobranchials.

Pectoral girdle moderately reduced (Fig. 6B). Posttemporal ventral ramus absent. Supracleithrum with weak, thinly ossified dorsal ramus and no cartilaginous lamina. Scapular foramen enclosed; scapular posterior ramus well developed. Four actinosts present, bearing pectoral fin rays on cartilaginous lamina opposite actinosts (no rays opposite scapula). Pelvic fin rays absent, pelvic bone reduced. Postcleithrum long, well ossified.

Epipleural ribs on vertebrae 1–16. Pleural ribs on third or fourth through ultimate or penultimate precaudal vertebrae. Dorsal fin origin associated with vertebrae four or five, with no free pterygiophores. All dorsal fin elements soft rays, first not segmented, but bilaterally divided near base. Last dorsal ray associated with second or fourth preural vertebra. Anal fin origin associated with last precaudal vertebra or first caudal vertebra, with zero to three ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. All anal fin elements soft rays (all segmented); last anal ray associated with second or third preural vertebra. Caudal fin rays six to eight, with one or two epural, two or three upper hypural, and three lower hypural rays.

Palatine membrane (oral valve) well developed, reaching anterior edge of vomer. Two small pseudobranch filaments. Pyloric caeca two small nubs, more regressed in one specimen than others. One gravid female (ZIL 41568, 59 mm) with only four ova measuring 3.1–4.1 mm in diameter.

Dorsal surface of head and body uniformly reddish brown; body mottled ventrally and posteriorly, especially below midline. Ventrally, background color blue in ISH 376/78, but Norman (1937) noted it to be "pale yellowish white" in holotype (in alcohol), a smaller specimen. Fins yellowish. Lining of orobranchial cavity pale.

Letholycus magellanicus sp. nov.

(Fig. 1C)

HOLOTYPE.—ISH 164/78 (144 mm SL); Argentine slope (45°59.3'S, 59°57.1'W); WH sta. 531/78; 580 m; 15 May1978.

PARATYPE.—ISH 173/78 (150 mm SL); Argentine slope (45°54.7'S, 59°43.9'W); WH sta. 533/78; 900 m; 15 May 1978.

COUNTS AND MEASUREMENTS.—Vertebrae 27 + 73–74 = 100–101; D 95–96; A 75–76; C 7; P1 13–14; P2 absent; vomerine teeth four to six; palatine teeth five to six; premaxillary teeth 10–15; dentary teeth 12–16; gill rakers 2 + 7 = 9; branchiostegal rays six; pseudobranch filaments two; pyloric caeca two. Following measurements in percent SL: head length 14.7–15.1; head width 5.3–6.4; pectoral fin length 6.5–6.7; predorsal length 16.9; preanal length 38.1–38.7; body height 8.8–9.2; caudal fin length 1.3–1.4. Following measurements in percent HL: head width 36.0–42.3; upper jaw length 39.6–42.2; pectoral fin length 44.0–44.1; snout length 22.7–23.1; eye diameter 21.1–21.3; gill slit length 32.2–35.1; interorbital width 9.5–9.7. Pectoral base/length ratio 51.6–56.0.

DIAGNOSIS.—Preoperculomandibular pores eight; suborbital pores five to six; postorbital pores three; mesial occipital pore present; pectoral fin rays 13–14; dorsal fin origin associated with third vertebra; body lateral line mediolateral, extending to tail tip; gill opening extending ventrally to lower edge of pectoral base or slightly above; pectoral base/length ratio 51.6–56.0.

DESCRIPTION.—Head relatively short, bluntly rounded anteriorly; ventral profile gently curved. Body moderately elongate, ovoid in cross section; profile not tapering posteriorly. Tail laterally compressed, especially posteriorly. Skin firm, moderately thickened, with slight, subdermal gelatinous layer about abdomen. Lateral line mediolateral, its origin just posterior to fourth postorbital pore, neuromasts extending to tail tip; lateral line coursing in straight line across abdomen. Scales minute, cycloid, imbedded, extending anteriorly to dorsal fin origin; in wedge-shaped pattern on dorsum, absent on abdomen, head, and pectoral base; scales present on vertical fins to about half their height posteriorly, less anteriorly (scales absent on anterior eighth of anal fin). Eyes moderately large, rounded. Gill opening bowed ventrally, with slight, posteriorly directed flap; extending to lower edge of pectoral base or to opposite pectoral rays 10–12. Single pair of nostrils at snout tip, nasal tube overlapping upper lip, but not extending beyond it. Pectoral fin evenly rounded posteriorly, moderately large, origin just below body midline, insertion on ventral surface of abdomen; all rays excised at tips, ventralmost more so than dorsalmost; ventral rays thickened.

Mouth moderately large, terminal. Teeth in jaws small, conical, in two short, irregular rows anteriorly, blending into single, posterior row. Teeth in palate larger, in patch on vomer and single row on palatine bone.

Cephalic lateralis pore system somewhat reduced numerically, pore enlarged, rounded. Two pairs of nasal pores, located just anteromesial and posteromesial nasal tube. First, third, and fourth postorbital pores present, emanating from frontals (first), pterotics (third), and lateral extrascapulars (fourth). Interorbital pore absent. Single, mesial occipital (supratemporal) pore present, supratemporal commissure complete across parietals. Preoperculomandibular canal with four dentary, one anguloarticular, and three preopercular pores. Five suborbital pores emanating from ventral branch of bone chain, paratype with a sixth from ascending branch just ventral to first postorbital pore.

Limited osteological observations made from radiographs and superficial dissection. Sphenotic and parietal separated by frontal and pterotic. Pterotic broadest at midlength, containing tubular passage for postorbital canal anteriorly. Supraoccipital moderately large, separated from exoccipital by epioccipitals. Parietals not meeting in midline. Single lateral extrascapular. Palatal arch weak, ectopterygoid and mesopterygoid contacting less than half dorsal and anterior surfaces of quadrate. Mandibular and preopercular lateralis canals joined. Ceratohyal–epihyal juncture smooth. Branchiostegal rays six: four articulating with ceratohyal, two with epihyal. Ceratobranchial five dentate. Three pair of infrapharyngobranchials present. Four actinosts bearing pectoral rays. Pelvic fins absent. Postcleithrum present. Dorsal fin origin associated with third vertebra, with no free pterygiophores. All dorsal fin elements soft rays, first not segmented, but bilaterally divided near base, remainder segmented. Last dorsal ray associated with third preural vertebra. Anal fin origin associated with last precaudal vertebra, with three or four ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. All anal fin

elements soft rays; last anal ray associated with second preural vertebra. Caudal fin rays seven, with one epural, three upper hypural, and three lower hypural rays.

Palatine membrane weak; very slight fold anteriorly, not reaching vomer. Two small pseudobranch filaments. Pyloric caeca two small nubs.

Dorsal surface of head, body, and tail reddish brown; tail mottled with reddish brown ventrally on blue background. Abdomen, ventral surface of head, and eye blue. Fins reddish brown. Lining of orobranchial chamber dark brown.

ETYMOLOGY.—Named after zoogeographic Magellan Province (Regan 1914; Briggs 1974), to which this species is presumably endemic. Province named honoring Spanish explorer Ferdinand Magellan, first European to visit these waters.

LITERATURE CITED

ANDERSON, M. E. 1982. Revision of the fish genera *Gymnelus* Reinhardt and *Gymnelopsis* Soldatov (Zoarcidae), with two new species and comparative osteology of *Gymnelus viridis*. Natl. Mus. Nat. Sci., Publ. Zool. 17:1–76.

———. 1984. On the anatomy and phylogeny of the Zoarcidae (Teleostei: Perciformes). Ph.D. Dissertation, College of William and Mary, Williamsburg, Virginia. 254 pp.

———. In press. 1988. Studies on the Zoarcidae (Teleostei: Perciformes) of the southern hemisphere. I. Ant. Res. Ser., Amer. Geo. Phys. Union. The Antarctic and subantarctic regions.

———. 1988. A new genus of California eelpout (Teleostei: Zoarcidae) based on *Maynea californica* Starks and Mann, 1911. Proc. California Acad. Sci. 45(5):89–96.

BRIGGS, J. C. 1974. Marine zoogeography. McGraw Hill, New York. 475 pp.

CUNNINGHAM, R. O. 1871. Notes on the reptiles, amphibia, fishes, mollusca and crustacea obtained during the voyage of H.M.S. "Nassau" in the years 1866–69. Trans. Roy. Soc. London 27(4):455–502.

DINGERKUS, G. AND L. D. UHLER. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Tech. 52(4):229–232.

GOSZTONYI, A. E. 1977. Results of the research cruises of FRV "Walther Herwig" to South America. XLVIII. Revision of the South American Zoarcidae (Osteichthyes, Blennioidei) with the description of three new genera and five new species. Arch. Fischereiss. 27(3):191–249.

GÜNTHER, A. 1880. Report on the shore fishes procured during the voyage of H.M.S. "Challenger" in the years 1873–1876. Rep. Sci. Res. Challenger 1(6):1–82.

LEVITON, A. E., R. H. GIBBS, JR., E. HEAL AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985(3):802–832.

MCALLISTER, D. E. AND E. I. S. REES. 1964. A revision of the eelpout genus *Melanostigma*, with a new genus and with comments on *Maynea*. Bull. Nat. Mus. Canada 199:85–109.

NORMAN, J. R. 1937. Coast fishes, part II. The Patagonian region. Discovery Rep. 16:1–130.

REGAN, C. T. 1913. The Antarctic fishes of the Scottish National Antarctic Expedition. Trans. Roy. Soc. Edinburgh 49(2): 229–292.

———. 1914. Fishes. Brit. Antarct. ("Terra Nova") Exped., 1910. Nat. Hist. Rept., Zool. 1(1):1–54.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES

Vol. 45, No. 12, pp. 277-317, 8 figs. December 7, 1988

THE MYRTLE FAMILY (MYRTACEAE) IN CHILE

By
Leslie R. Landrum

Department of Botany, Arizona State University, Tempe, Arizona 85287[1]

ABSTRACT: **This paper is a floristic treatment of the Myrtle family (Myrtaceae) in Chile. The family is represented by nine genera and 26 species: *Amomyrtus* (2 spp.), *Blepharocalyx* (1 sp.), *Legrandia* (1 sp.), *Luma* (2 spp.), *Myrceugenia* (14 spp.), *Myrcianthes* (1 sp.), *Myrteola* (1 sp.), *Tepualia* (1 sp.), and *Ugni* (3 spp.). Keys to the genera and species are provided, as are descriptions, lists of synonyms, distribution maps, illustrations of most species, and notes on distribution, phenology, local names and uses, and similar or closely related taxa.**

Received September 21, 1987. Accepted February 3, 1988.

NUMERICAL LIST OF TAXA

1. *Tepualia*
   1.1. *T. stipularis* Grisebach
2. *Myrcianthes*
   2.1. *M. coquimbensis* (Barnéoud) Landrum et Grifo
3. *Amomyrtus*
   3.1. *A. luma* (Molina) Legrand et Kausel
   3.2. *A. meli* (R. A. Philippi) Legrand et Kausel
4. *Blepharocalyx*
   4.1. *B. cruckshanksii* (W. J. Hooker et Arnott) Niedenzu
5. *Legrandia*
   5.1. *L. concinna* (R. A. Philippi) Kausel
6. *Myrteola*
   6.1. *M. nummularia* (Poiret) Berg
7. *Ugni*
   7.1. *U. candollei* (Barnéoud) Berg
   7.2. *U. molinae* Turczaninow
   7.3. *U. selkirkii* (W. J. Hooker et Arnott) Berg
8. *Myrceugenia*
   8.1. *M. chrysocarpa* (Berg) Kausel
   8.2. *M. colchaguensis* (R. A. Philippi) Navas
   8.3. *M. correifolia* (W. J. Hooker et Arnott) Berg
   8.4. *M. exsucca* (A. P. de Candolle) Berg
   8.5. *M. fernandeziana* (W. J. Hooker et Arnott) Johow
   8.6. *M. lanceolata* (Jussieu ex Jaume Saint-Hilaire) Kausel
   8.7. *M. leptospermoides* (A. P. de Candolle) Kausel
   8.8. *M. obtusa* (A. P. de Candolle) Berg
   8.9. *M. ovata* (W. J. Hooker et Arnott) Berg
      8.9a. var. *ovata*
      8.9b. var. *nannophylla* (Burret) Landrum

[1] This work partially completed as Tilton Fellow, Department of Botany, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118.

8.10. *M. parvifolia* (A. P. de Candolle) Kausel
8.11. *M. pinifolia* (F. Philippi) Kausel
8.12. *M. planipes* (W. J. Hooker et Arnott) Berg
8.13. *M. rufa* (Colla) Skottsberg ex Kausel
8.14. *M. schulzei* Johow
9. *Luma*
9.1. *L. apiculata* (A. P. de Candolle) Burret
9.2. *L. chequen* (Molina) A. Gray

Introduction

The purpose of this paper is to present all the information necessary for the proper identification of Chilean Myrtaceae. Most of the genera have already been monographed (Landrum 1981, 1986, 1988) and monographs are being prepared for *Ugni* and *Amomyrtus*. However, these papers are scattered and do not deal exclusively with Chilean Myrtaceae. In the present paper I wish to leave out, for most species, much information included in a monograph, such as: discussions of intergeneric relationships and nomenclatural history; citation of type specimens; treatment of non-Chilean species; and lists of representative specimens. The keys and discussion of the present paper have been designed for one dealing only with the Chilean flora.

There has been no comprehensive treatment of the family in Chile since the work of Reiche (1897), well before modern concepts of genera and species of Chilean Myrtaceae had been formed. Kausel (1942, 1944, 1948, 1949) wrote a series of very useful papers on Chilean Myrtaceae but he never published a family treatment in a single paper. Navas (1970) provided a key to the species represented in SGO (Museo de Historia Natural, Santiago, Chile) and cited the specimens housed there. Her work is largely based on the publications of Kausel.

The Myrtaceae of Chile are found from coastal Coquimbo to the southern tip of South America. They grow in the humid temperate forests of southern Chile and adjacent Argentina and in the Mediterranean sclerophyllous vegetation of central Chile. The Myrtaceae of Chile and adjacent southwestern Argentina are growing in a climatic and vegetational island bounded by very dry deserts in the north and east and oceans to the west and south. The forest vegetation of southwestern Argentina is essentially the same as that found in southern Chile, all the Myrtaceae of the region growing in Chile as well. The keys and descriptions in this paper are equally applicable to Myrtaceae of southwestern Argentina and the distribution maps include that region.

The phytogeographic relationships of the Myrtaceae of Chile will be the subject of another paper but will be summarized here. Nine genera of Myrtaceae are found in the above-described climatic and vegetational island: *Legrandia, Luma,* and *Amomyrtus* are endemic and have no clear relationships in other regions. *Myrceugenia, Blepharocalyx,* and *Myrcianthes* have disjunct distributions across South America, other species being found in eastern temperate and subtropical Brazil, Paraguay, Uruguay, and northeastern Argentina. *Tepualia, Ugni,* and *Myrteola* are closely related to genera of Australasia. *Blepharocalyx, Myrcianthes, Ugni,* and *Myrteola* have disjunct populations in the Andes of northern Argentina and/or farther north.

MYRTACEAE A. L. Jussieu, 1789

The Myrtaceae can be distinguished from other families by having (1) persistent leaves with entire margins; (2) usually whitish flowers with inferior ovaries and numerous stamens; and (3) unlignified portions of the plant dotted with glands containing viscous aromatic substances (terpenoids and polyphenols). All the native Chilean Myrtaceae have opposite leaves, but the commonly cultivated genus *Eucalyptus* of Australia has alternate leaves at maturity.

Myrtaceae have traditionally been divided into two tribes or subfamilies based on fruit structure: Leptospermeae (or Leptospermoideae) with dry, usually capsular fruits; and Myrteae (or Myrtoideae) with fleshy, berry fruits. Only one capsular fruited species occurs in America, *Tepualia stipularis.* The Myrteae are divided into subtribes based on embryo structures described below.

The following description is applicable to native Chilean Myrtaceae only.

Subshrubs, shrubs, or trees to about 20 m high, usually aromatic, sometimes strongly so, usually growing in relatively humid habitats, the trunks often with smooth or scaly bark, often orangish or light brown to white; hairs unicellular, simple or dibrachiate (two armed). Leaves persistent, coriaceous to submembranous, opposite, the venation usually brochidodromous, i.e., with a

strong midvein and lateral veins connected by arches near the margin, the connecting arches termed the marginal vein; inflorescence uniflorous (Fig. 10A), a dichasium (Fig. 1A, D, E), or a bracteate shoot (Fig. 3A) of uniflorous peduncles (i.e., a raceme), the peduncles solitary or sometimes (especially in *Myrceugenia*) superimposed in pairs or triplets in the axils of leaves; flowers pentamerous or tetramerous, whitish or sometimes pinkish in *Ugni*; stamens usually numerous (as few as 9 in *Myrteola*), the anthers laterally dehiscent (or introrsely dehiscent in *Ugni*); ovary inferior, 2–4-locular; placentation axil (sometimes appearing apical) or basal (in *Tepualia*), the ovules few to numerous, biseriate or multiseriate. Fruit a locucidal capsule in *Tepualia,* otherwise a berry; seeds 1–several, linear in *Tepualia,* subglobose, lenticular, or reniform in berry-fruited genera, the seed coats membranous to hard and stony; embryo linear in *Tepualia,* variable, and of great taxonomic importance in the berry-fruited genera, the following types being found: (1) the hypocotyl about as long as or longer than the linear to oblong cotyledons (*Amomyrtus, Blepharocalyx, Legrandia, Myrteola, Ugni* of subtribe Myrtinae) (Fig. 3H); (2) the cotyledons leafy and folded in a bundle around which is wrapped the hypocotyl (*Myrceugenia* of subtribe Myrciinae) (Fig. 11A); (3) the cotyledons thick, planoconvex, and the hypocotyl insignificant (*Myrcianthes* of subtribe Eugeniinae); (4) the slightly fleshy, suborbicular cotyledons of about equal length as the hypocotyl (*Luma* of uncertain affinities) (Fig. 11B).

Key to Genera for Fruiting Specimens

1. Fruit a capsule ..... 1. *Tepualia*
1. Fruit a berry
   2. Subshrub, creeping along the surface or up to ca. 1 m high; leaves mainly less than 1 cm long, bullate beneath, the lower epidermis becoming detached; seeds less than 2 mm long; bracteoles persistent, foliaceous; calyx lobes 4–5 on the same plant ..... 6.1. *Myrteola nummularia*
   2. Trees or shrubs often over 1 m high; some leaves normally over 1 cm long, not bullate, the lower epidermis never becoming detached; seeds over 2 mm long (except in *Ugni*); bracteoles and calyx various
      3. Calyx lobes 4
         4. Fruit ca. 1.5–2.5 cm in diameter, yellowish; seed ca. 1.3–2 cm long, the embryo essentially a solid ellipsoidal to subglobose mass, the cotyledons insignificant; Andes below ca. 1,000 m from Curicó to Ñuble ..... 5.1. *Legrandia concinna*
         4. Fruit up to ca. 1 cm in diameter, variously colored; seed up to ca. 0.6 cm long, the embryo never a solid ellipsoidal or subglobose mass, the cotyledons making up at least half the embryo (except in *Blepharocalyx*)
            5. Ripe fruit orange, yellow, or reddish; cotyledons leafy, folded into a bundle; hypocotyl long, encircling the cotyledons ..... 8. *Myrceugenia*
            5. Fruit purple to black; embryo various
               6. Bracteoles persistent until the fruit matures; fruit usually maturing 2–12 mo after anthesis; cotyledons folded into a bundle, membranous; hypocotyl encircling the cotyledons (Fig. 11A) ..... 8. *Myrceugenia*
               6. Bracteoles caducous at about anthesis; fruit usually maturing soon after anthesis; cotyledons not folded into a bundle, membranous or fleshy; hypocotyl not encircling cotyledons
                  7. Leaf apex acute or acuminate; cotyledons about round, as long as the hypocotyl (Fig. 11B) ..... 9. *Luma*
                  7. Leaf apex obtuse to emarginate; cotyledons narrow, much shorter than the hypocotyl ..... 4. *Blepharocalyx*
      3. Calyx lobes 5 (or mainly 5 and less often 4 on the same plant in *Ugni*)
         8. Bracteoles persistent until fruit matures; seed ca. 1–2 mm long, the seed coat hard ..... 7. *Ugni*

8. Bracteoles caducous at about anthesis; seed more than 2 mm long, the seed coat hard or membranous
9. Leaves 1.4–3.5 times as long as wide; apex often mucronate; margin not revolute; seed coat hard; hypocotyl much longer than cotyledons; Concepción to Aisén ..... 3. *Amomyrtus*
9. Leaves 0.9–1.6 times as long as wide; apex never mucronate; margin often revolute; seed coat soft; cotyledons much longer than hypocotyl; coast of Coquimbo ..... 2.1. *Myrcianthes coquimbensis*

Key to Genera for Flowering Specimens

1. Flowers pentamerous, or tetramerous and pentamerous on the same plant in *Myrteola* and *Ugni*
   2. Bracteoles persistent until after anthesis
      3. Filaments 5–10 times as long as the subglobose anthers; stamens exserted; flowers erect ..... 6.1. *Myrteola nummularia*
      3. Filaments 1–3 times as long as the sagitate anthers; stamens included; flowers nodding ..... 7. *Ugni*
   2. Bracteoles (at least the great majority) caducous at or before anthesis
      4. Two corky epidermal protrusions present on the twig at the base of most petioles, these stipule-like; leaves lanceolate, usually no more than 1.5 cm long, the lower epidermis of the leaf often wrinkled, often becoming detached, bullate ..... 1.1. *Tepualia stipularis*
      4. No corky epidermal protrusions present; leaves various, often over 1.5 cm long, the lower epidermis not wrinkled, not becoming detached, not bullate
         5. Leaves 1.4–3.5 times as long as wide; apex often mucronate; margin not revolute; peduncles ca. 0.3–0.5 mm wide, uniflorous, often grouped together in bracteate shoots (racemes); Concepción to Aisén ..... 3. *Amomyrtus*
         5. Leaves 0.9–1.6 times as long as wide; apex never mucronate; margin often revolute; peduncles ca. 1 mm wide at middle, uniflorous or triflorous, not grouped together in bracteate shoots (racemes); coast of Coquimbo ..... 2.1. *Myrcianthes coquimbensis*
1. Flowers tetramerous
   6. Subshrub, creeping along the surface or up to ca. 1 m high; leaves mainly less than 1 cm long, bullate beneath; stamens up to ca. 16 ..... 6.1. *Myrteola nummularia*
   6. Trees or shrubs often over 1 m high; some leaves normally over 1 cm long, not bullate, the lower epidermis never becoming detached; stamens rarely less than 20
      7. Bracteoles foliaceous, caducous at about anthesis, elliptic, ca. 7–9 mm long, 2–4 mm wide; disk ca. 6 mm across; style ca. 9–12 mm long; Andes from Curicó to Ñuble at about 700–1,000 m ..... 5.1. *Legrandia concinna*
      7. Bracteoles not foliaceous (except in *Myrceugenia obtusa,* or rarely in *M. correifolia,* then only 2–7 mm long); disk up to ca. 4 mm across; style usually less than 9 mm long
         8. Bracteoles persistent until after anthesis, normally until fruit matures ..... 8. *Myrceugenia*
         8. Bracteoles caducous at or before anthesis
            9. Leaf apex obtuse to emarginate; twigs often 4-angled; hairs dibrachiate; ovules multiseriate ..... 4.1. *Blepharocalyx cruckshanksii*
            9. Leaf apex acute or acuminate; twigs not 4-angled; hairs simple; ovules normally biseriate
               10. Leaves lanceolate to ovate, 2.8–7.3 cm long; petiole 2–5 mm long; peduncles uniflorous, mainly borne in bracteate shoots (racemes); Masatierra, Juan Fernández ..... 8.5. *Myrceugenia fernandeziana*
               10. Leaves mainly elliptic to suborbicular, 0.5–4.5 cm long; petiole 0.5–2 mm long; peduncles uniflorous or bearing dichasia, only rarely borne in bracteate shoots; mainland Chile and adjacent Argentina ..... 9. *Luma*

LEPTOSPERMEAE A. P. de Candolle, 1826

1. **Tepualia** Grisebach, Sys. Bemerk. 31. 1854; Abh. Königl. Ges. Wiss. Göttingen 6:119. 1854.

Tepualia consists of a single species endemic to the forests of central and southern Chile and adjacent Argentina. I have not treated it in any other paper and thus cite types and representative specimens here.

1.1. **Tepualia stipularis** (W. J. Hooker et Arnott) Grisebach, Syst. Bemerk. 31. 1854; Abh. Königl. Ges. Wiss. Göttingen 6:119. 1854.

Myrtus stipularis W. J. Hooker et Arnott, Bot. misc. 3:316. 1833. Type. Chile. "Chiloe," *Cuming 32* and *33* (syntypes at E-GL, *Cuming 32* hereby designated as lectotype; *Cuming 33*, isoparatype, W; NY neg. 10835 of lectotype and paratype at E-GL).

Metrosideros stipularis (W. J. Hooker et Arnott) J. D. Hooker, Fl. antarct. 275. 1844.

Tepualia philippiana Grisebach, Syst. Bemerk. 32. 1854; Abh. Königl. Ges. Wiss. Göttingen 6:120. 1854. Type. Chile. "Valdivia: in Cordillera," *Philippi 89* (holotype, GOET, n.v.; isotype, W; F neg. 23484 of isotype at G).

Tepualia patagonica R. A. Philippi, Anales Univ. Chile 84: 755. 1893. Type. Chile. Magallanes: "Habitat in Patagonia occidentali, loco dicto Rindgdove Inlet in latit. austr. 49°49′ et longit. 74°15′; Januario 1879 reperta," collector? (holotype, SGO, n.v.).

Tepualia stipularis var. *patagonica* (R. A. Philippi) Reiche, Anales Univ. Chile 98:726. 1897; Fl. Chile 2:310. 1898.

Tepualia stipularis var. *philippiana* (Grisebach) Spegazzini, Anales Mus. Nac. Hist. Nat. Buenos Aires 7:284. 1902.

Shrub or small tree up to ca. 7 m high, glabrous to minutely and obscurely puberulent; hairs simple, whitish, ca. 0.1 mm long; twigs glabrous to minutely and sparsely puberulent when young, glabrescent with age, chestnut brown at first, later becoming greyish to reddish brown, scaly, more or less 4-angled when young, the angles expanding into auriculate appendages lateral to the petiole bases, the appendages up to ca. 2 mm long, the longest produced at the beginning of a season's growth, those at later nodes progressively smaller, the buds covered with scales. Leaves lanceolate, ovate, elliptic, or suborbicular, 3–13 mm long, 2–6 mm wide, 1–4 times as long as wide, glabrous, the lower epidermis often becoming detached and bullate (at least in drying); apex obtuse; base rounded to subcordate; petiole more or less flat above, glabrous to sparsely puberulent, 1–2 mm long, 0.5–0.7 mm wide, ascending along twig; midvein indistinct to faintly visible; lateral veins indistinct or 2–3 pairs faintly visible, strongly ascending, nearly parallel to the midvein; marginal veins indistinct; blades dotted with glands, yellow green to grey green above, somewhat lighter and often tinged with brown below, subcoriaceous, the margins usually slightly revolute. Peduncles uniflorous, 2–9 mm long, ca. 0.5 mm wide, glabrous to sparsely puberulent, elongating and becoming curved as fruit matures, the bracteoles attached ca. 1–4 mm below the hypanthium; bracteoles linear, ca. 1–2 mm long, usually caducous before or at anthesis; calyx lobes 5, more or less triangular, ca. 1 mm long, ca. 2 mm wide; petals 5, ca. 2 mm long, suborbicular to obovate; hypanthium campanulate, 1.5–2.5 mm long, with 5 longitudinal ridges; disk ca. 2.5 mm across; style 6–8 mm long, glabrous, gynobasic; stamens 15–24, uniseriate, 4–8 mm long; anthers ca. 0.5 mm long; ovary (2–)3(–4)-locular; ovules 5–22, basally attached, linear, about as long as locule. Fruit a locucidal capsule ca. 3 mm long; seeds linear, released through the top of the capsule, the sides of the capsule later wearing away between the ribs of the hypanthium (Fig. 1A, B).

DISTRIBUTION (Fig. 2A).—A tree or shrub of wet habitats, from Maule and Ñuble and then more or less continuously from Cautín to Magallanes in Chile; and from the Andean forests of Río Negro, Chubut, and Santa Cruz in Argentina.

REPRESENTATIVE SPECIMENS.—ARGENTINA. Chubut: Lago Menéndez, Lago Futalaufquén, 20 Jan 1938 (fl), *Kalela 1833* (H). Río Negro: Nahuel Huapi, orilla occidental de la Laguna Frías, 28 Apr 1942 (fl), *Diem 356* (CONC); Lago Nahuel Huapi, frente a Puerto Blest, 19 Jan 1940 (fl), *Perez Moreau 34071* (H). Santa Cruz: Lago San Martín, Bajo Esperanza, 11–16 Apr 1944 (fr), *Grosse 43* (CONC, H).

CHILE. Aisén: Isla Ofhidro (48°28′S, 74°05′W), 17 Jan 1968 (fl), *Anliot 6044* (SGO); Puerto Aisén, 22 Jan 1962 (fl), *Behn s.n.* (CONC); Bahía Chantel, desembocadura del Río Baker, 8 May 1949 (fr), *Grosse s.n.* (CONC); Península Taitao, Estero Puelma (fl), *Grosse 127* (SGO); Islas Chonos, Puerto Americano, 28 Feb 1921 (fl), *Hicken s.n.* (US); Isla Rivero, Estero Balladares (45°44′S, 74°21′W), 20 Jul 1970 (fr), *Parra 71* (CONC); Tortel, frente a Canal Montalva (47°50′S, 73°34′W), 5 m, 5 Aug 1976 (fr), *Rodríguez 816* (CONC); Rada Quesahuén, 25 m, Feb 1959 (fl), *Schlegel 2053* (CONC); Estuario Elefantes, Puerto Bonito (45°56′S, 73°35′W), 30 m, 21 Feb 1967 (fl), *Seki 186* (CONC); Río Exploradores entre Río Verde y Río Teresa (46°25′S, 73°20′W), 20 m, 2 Mar 1967 (fl), *Seki 317* (CONC). Cautín: Conguillío, May 1972 (fl), *Weber s.n.* (EIF). Chiloé: Castro, Fundo Piruquina, 28 Jan 1933 (fl), *Behn s.n.* (CONC); camino a Chepu, 8 May 1972 (fr), *Landrum s.n.* (EIF); Quemchi, 11 May 1972 (fr), *Landrum s.n.* (EIF); Yaldad, ca. 10 km W of Quellón, 1–5 m, 7 Feb 1978 (fl), *Landrum 3131* (MICH, VALD); Chaitén, 19 Feb 1961 (fl), *Marticorena*

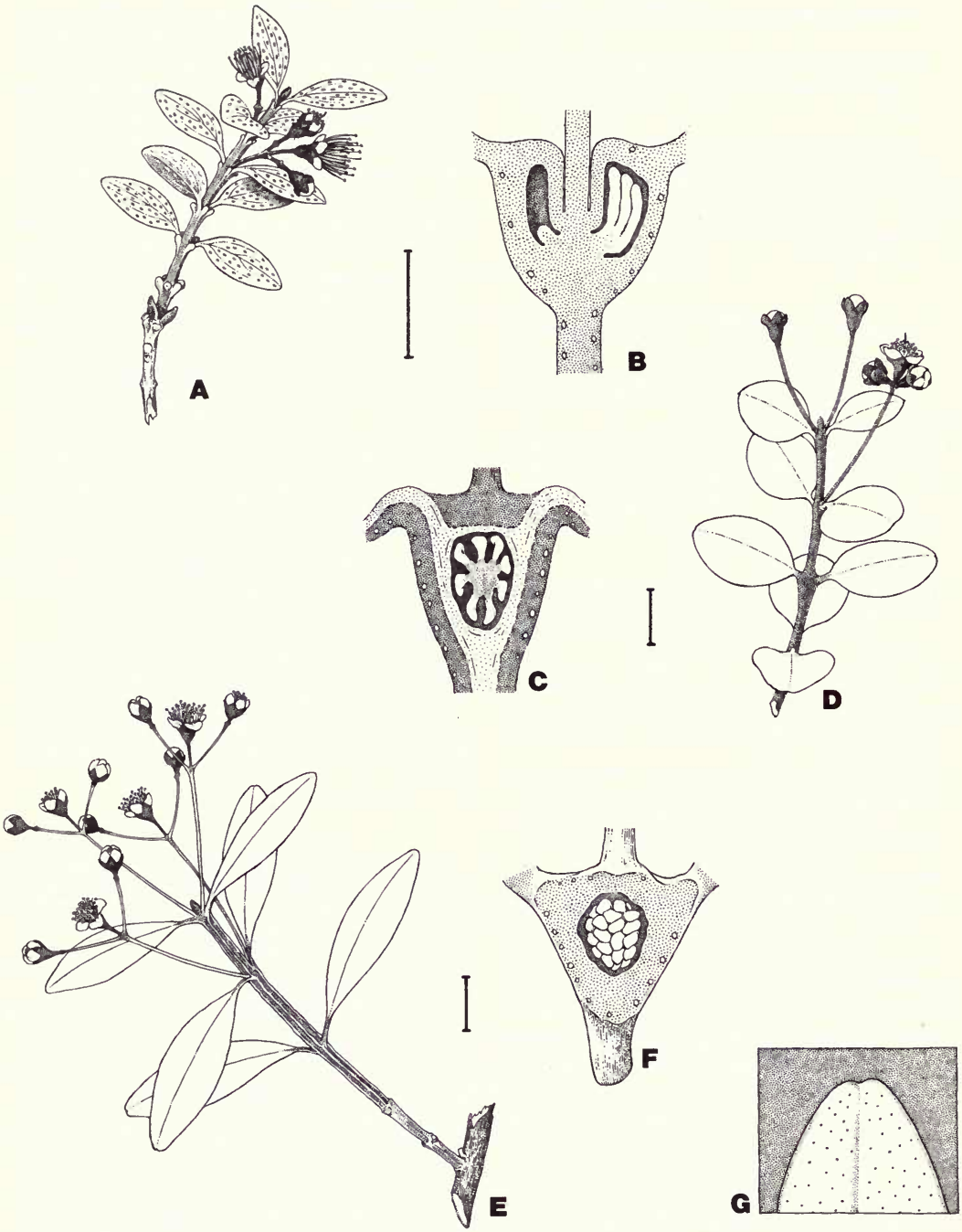


FIGURE 1. *Tepualia, Myrcianthes,* and *Blepharocalyx. Tepualia stipularis* (*Pisano 1260* at H): A, a twig with flowers and buds showing epidermal appendages at the bases of leaves. B, section of ovary showing basally attached ovules and gynobasic style. *Myrcianthes coquimbensis* (*Grosse s.n.,* 25 Oct 1946, at US): C, section of ovary showing peltate placenta. D, twig showing uniflorous and triflorous peduncles. *Blepharocalyx cruckshanksii* (*Werdermann 301* at CAS): E, 4-angled twigs with dichasial inflorescences. F, section of ovary showing irregular rows of ovules. G, leaf tip showing emarginate apex. Bars = 1 cm for twigs and 1 mm for sections. Drawn by Terry Bell.

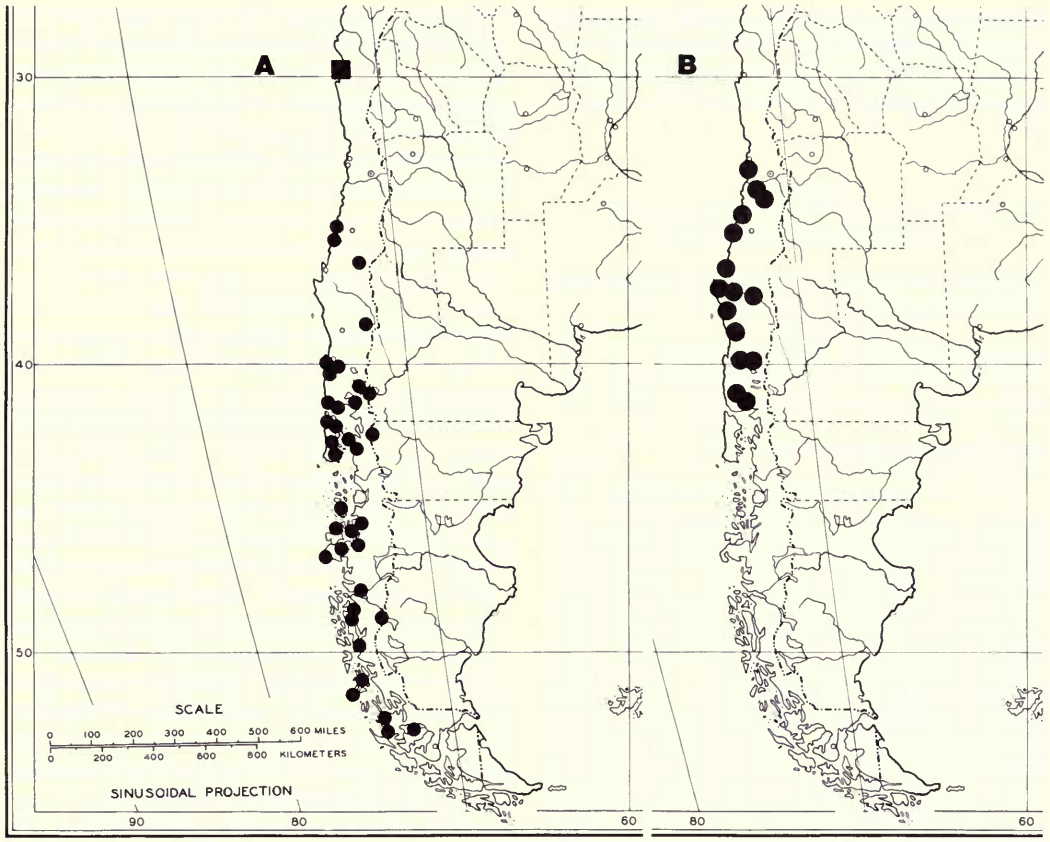


FIGURE 2. Distribution of *Tepualia stipularis* (A, circles), *Myrcianthes coquimbensis* (A, square), and *Blepharocalyx cruckshanksii* (B, circles).

1694 (CONC); Estero Palvitad, 25 Feb 1961 (fl), *Marticorena 1754* (CONC); Lago Natri, frente a Miraflores (42°47′S, 73°50′W), 85 m, 11 Jan 1975 (fl), *Marticorena et al. 63* (CONC); Isla Tranqui, Jan 1952 (fl), *Ramírez s.n.* (CONC); Islas Guaytecas, Melinka, 7 Feb 1957 (fr), *Ricardi et al. 4041* (CONC); Quinchao, Isla Talcán (42°46′S, 72°56′W), 30 m, 20 Feb 1972 (fr), *Urbina and Riffo s.n.* (CONC). Llanquihue: camino a Calbuco, 17 Dec 1970 (fr), *Gajardo s.n.* (EIF); desembocadura del Río Maullín, entre Chanhue y Lepihue, orillas del mar, 26 Nov 1944 (st), *Kausel 1509* (H); Ensenada, 13 Feb 1964 (fl), *Kausel 4728* (H); faldeos Volcán Osorno, frente al Lago Todos Los Santos, 520 m, 27 Jan 1972 (fl), *Rodríguez 20* (CONC). Magallanes: Hammick (48°44′S, 74°20′W), 4 Jan 1968 (fl), *Anliot 6043* (SGO); Isla Fairway, Canal Smith, 16 Mar 1945 (fl), *Biese 1335* (SGO); Isla Diego de Almagro, Pelantaro, 28 Mar 1945 (fl), *Biese 1543* (SGO); Port Otway, 9 Feb 1888 (fl), *Lee s.n.* (US); Puerto Edén, 23 Jul 1970 (fr), *Parra 99* (CONC); Puerto Bueno, 26 Jul 1970 (st), *Parra 157* (CONC); Seno de Skyring, al pié del Monte Cupulo, 27 Apr 1908 (fl), *Skottsberg s.n.* (SGO); Canal Smith, Feb 1924 (fl), *Skottsberg 133* (W). Maule: Constitución, Quebrada Honda, 7 Feb 1949 (fl), *Kausel 2733* (H); camino Cauquenes a Pelluhue, Mar 1971 (fr), *Landrum and Donoso s.n.* (EIF, SGO). Ñuble: entre San Fabián de Alico y Los Sauces, 4 km antes de Los Sauces, 15 Oct 1970 (fr), *Weldt 476* (CONC). Osorno: summit of Cordillera de la Carpa, 950 m, 1–3 Feb 1958 (fr), *Eyerdam 10564* (US); Puyehue, camino a Antillanca, 22 Feb 1971 (fl), *Landrum s.n.* (EIF). Valdivia: Cordillera Pelada de Chaihuín, 400 m, 3 Jan 1932 (fl), *Gunckel 3020* (H); Hueicolla, ca. 150 m, 17 Apr 1982 (fr), *Landrum 4501* (NY, SGO); La Unión, Llancacura, Jan 1969 (fl), *Mahú 2013* (H); orillas del Río Chamil, 19 Jan 1972 (fl), *Mahú 8366* (H).

PHENOLOGY.—Flowering mainly from January to March; fruits maturing mainly from May to August.

LOCAL NAMES.—Tepu, trepu, tepual (for a forest) (Muñoz 1966).

Tepualia stipularis is superficially similar to *Myrteola nummularia* as a dried specimen, but is easily distinguished from all other Chilean Myrtaceae by its capsular fruits and the protuberant outgrowths of twig epidermis at the bases of its leaves.

Dawson (1972) has accepted *Tepualia* as a distinct monotypic genus in the subtribe Metrosi-

derinae. He believes that it is most closely related to *Mearnsia* Merrill of the Philippines, New Guinea, the Solomon Islands, New Caledonia, and New Zealand.

Myrteae

Eugeniinae Berg, 1856

2. **Myrcianthes** Berg, Linnaea 27:136 (in key), 315. Jan 1856.

Anamomis Grisebach, Fl. Brit. W.I. 240. 1860.
Reichea Kausel, Revisión de las Mirtáceas Chilenas 1. 1940.
Aspidogenia Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:522. 1941.
Acreugenia Kausel, Ark. Bot. 3:510. 1956.

Trees or shrubs, at least sometimes with smooth, somewhat scaly bark; hairs simple, unicellular. Leaves opposite or ternate, persistent, sometimes strongly coriaceous. Inflorescence typically a dichasium of 3–7 flowers, less often reduced to a single flower, the peduncles borne in the axils of leaves, solitary or rarely superimposed; flowers pentamerous or tetramerous; bracteoles caducous or persistent; ovary usually bilocular, the placenta attached to the central or upper part of the septum, the ovules 5–20 per locule. Fruit a berry, the seeds usually 1–2, the testa membranous; embryo subglobose, the cotyledons planoconvex, ununited, the hypocotyl small, shorter than the cotyledons.

Myrcianthes is widespread in subtropical eastern South America and in the Andes from northern Argentina to Venezuela. Two species are known from Central America, and one of these also grows in the Caribbean.

2.1. **Myrcianthes coquimbensis** (Barnéoud) Landrum et Grifo, Brittonia 40(3):290. 1988.

Myrtus coquimbensis Barnéoud, *in* Gay, Fl. Chil. 2:382. 1847. Type. Chile. Coquimbo: "orilla del mar," *Gay s.n.* (lectotype, P, designated by Landrum and Grifo, 1988; isolectotype, F—fragment; photo of lectotype, SGO-4478).
Reichea coquimbensis (Barnéoud) Kausel, Revisión de las Mirtáceas Chilenas 1. 1940.
Aspidogenia coquimbensis (Barnéoud) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:522. 1941.

Low, dense, rounded shrub usually ca. 1.5 m high, strongly glandular, glabrous or sometimes densely pubescent on young growth; hairs simple, straight or curved, grayish, mainly antrorse, up to ca. 0.3 mm long; twigs glabrous or sparsely to densely pubescent at first, losing any hairs with age, the young bark dark to light reddish brown, smooth, with age becoming grey and slightly rough. Leaves elliptic, ovate, obovate, or suborbicular, 1–3.4 cm long, 0.6–3 cm wide, 0.9–1.6 times as long as wide, glabrous to densely covered with hairs when young, usually becoming glabrous with age; apex acute, rounded, or emarginate; base acute, rounded, or subtruncate; petiole 1–4 mm long, 1–1.5 mm wide, densely pubescent to glabrous; midvein flat or nearly so above, moderately prominent below; lateral veins indistinct or up to ca. 6 pairs faintly visible, these nearly perpendicular to the midvein; marginal veins indistinct; blades stiffly and thickly coriaceous, usually somewhat revolute, drying grey green to light reddish brown, somewhat lighter below, sometimes lustrous above, sometimes blue green above (due perhaps to an epiphytic alga or lichen). Peduncles solitary, uniflorous or triflorous, 0.5–3 cm long, ca. 1 mm wide near middle, up to ca. 2 mm wide at apex, densely pubescent to glabrous; bracteoles linear, 1–2 mm long, ca. 0.2 mm wide, persisting until about anthesis; calyx lobes 5, unequal, subtriangular to hemiorbicular, usually 2, 1–1.5 mm long, and 3, 2–2.5 mm long; petals 5, oblong to suborbicular, ca. 5–6 mm long, glabrous except for a ciliate margin; hypanthium obconic to campanulate, 3–4 mm long, glabrous to densely pubescent, strongly glandular; disk 3–5 mm across, glabrous or pubescent; style 7–10 mm long, glabrous; stamens ca. 140–150, 6–10 mm long; anthers 0.3–0.5 mm long; ovary 2-locular; ovules 5–11 per locule, radiating from a shortly stalked subpeltate placenta attached to about the center of the septum. Fruit subglobose, 1–2 cm in diam.; seeds usually 1, ca. 1–1.5 cm thick (Fig. 1C, D).

Distribution (Fig. 2A).—*Myrcianthes coquimbensis* has a rather restricted distribution in Coquimbo, being known to grow only along the coast from about 20 km south of La Serena (Tortoralillo) to about 40 km north of the same city (Punta Calavera) (Landrum and Grifo 1988). It is a dense, rounded shrub, typically growing among large granitic boulders on ocean-facing slopes that receive almost constant cool moist breezes from the Pacific.

Phenology.—Flowering October to December. Fruits may require several months to mature.

Local Names.—Arrayán, lucumillo, lucumilla (Muñoz 1966).

Myrcianthes coquimbensis is easily distinguished from other species of Chilean Myrtaceae by a combination of pentamerous flowers and strongly coriaceous leaves with revolute margins.

This species has only recently been transferred to *Myrcianthes* (Landrum and Grifo 1988). Many specimens may still be found in herbaria under *Reichea* or *Myrtus*.

Myrtinae

3. **Amomyrtus** (Burret) Legrand et Kausel, Lilloa 13:145. ("1947") 1948.

Pseudocaryophyllus Berg, sect. *Amomyrtus* Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:514. 1941.

Aromatic shrubs or trees up to ca. 20 m high, with smooth or somewhat scaly bark; hairs simple, unicellular. Leaves opposite, persistent, coriaceous, usually lanceolate or ovate. Inflorescence a solitary flower or bracteate shoot of ca. 6 flowers, the peduncles solitary (or rarely superimposed); flowers pentamerous; bracteoles caducous at or before anthesis; ovary 2–3-locular, the placenta attached to the upper septum, more or less shield-shaped, the ovules radiating from the placental margin; fruit a berry, the seeds hard, few, shaped like a snail's shell with a single coil, 4–6 mm long; embryo C-shaped, the cotyledons short, folded back against the hypocotyl.

Amomyrtus is distinguished from all other genera of Chilean Myrtaceae by its pentamerous flowers, hard seeds 4–6 mm long, and strongly aromatic leaves.

Both species of *Amomyrtus* have very hard wood that is utilized for tool handles and lumbering and farming equipment or wherever very strong wood is needed.

Key to the Species of *Amomyrtus*

1. Trunk reddish brown with lighter spots; twigs densely to moderately pubescent; leaves moderately aromatic, seldom over 3 cm long or 1.5 cm wide; calyx lobes linear, linear oblong, or narrowly triangular; seed 4–4.5 mm long, grey green; hypanthium 2–2.5 mm long, not noticeably glandular; usually growing near water ..... 3.1. *A. luma*
1. Trunk more or less uniformly whitish; twigs obscurely pubescent to glabrous; leaves strongly aromatic, often over 3 cm long and 1.5 cm wide; calyx lobes approximately triangular, slightly wider than long; seed ca. 5–6 mm long, whitish; hypanthium 2.5–3.5 mm long, strongly glandular; usually growing as an understory tree in upland habitats ..... 3.2. *A. meli*

3.1. **Amomyrtus luma** (Molina) Legrand et Kausel, Lilloa 13:146. ("1947") 1948.

Myrtus luma Molina, Sag. stor. nat. Chili, ed. 1, 173. 1782.
Myrtus multiflora Jussieu ex Jaume Saint-Hilaire, *in* Duhamel, Traité arbr. arbust., ed. 2, 1:208. 1800–1803.
Eugenia darwinii J. D. Hooker, Fl. antarct. 277. 1846.
Myrtus darwinii (J. D. Hooker) Barnéoud, *in* Gay, Fl. Chil. 2: 383. 1847.
Myrcia lechleriana Miquel, Linnaea 25:651. 1852.
Myrtus valdiviana R. A. Philippi, Linnaea 28:688. 1858.
Pseudocaryophyllus darwinii (J. D. Hooker) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:514. 1941.

Shrub or tree up to ca. 20 m high, moderately aromatic, moderately to densely pubescent on young growth, the trunk smooth, reddish brown with lighter large spots where the bark has recently fallen; hairs whitish, most ca. 0.3–0.5 mm long, erect to antrorse; twigs densely to moderately pubescent, the bark at first light reddish brown to grey, with age splitting in a reticulate pattern, revealing reddish brown inner bark. Leaves elliptic, elliptic-oblong, ovate, or lanceolate, 1.4–2(–5) cm long, 0.6–1.5(–2.5) cm wide, 1.5–3 times as long as wide, essentially glabrous except for the midvein that is usually pubescent above; apex acute to abruptly acuminate or rounded, often mucronate; base acute or cuneate; petiole unchanneled to shallowly channeled, 2–4 mm long, 0.5–1 mm wide, densely pubescent to glabrous; midvein flat to slightly raised, prominent below; lateral veins indistinct or up to ca. 10 pairs faintly visible; marginal veins more or less equalling the laterals in prominence, paralleling the margin; blades usually stiffly coriaceous, drying grey green to dark reddish brown, often with many recessed pores above. Peduncles solitary, 0.5–2 cm long, 0.3–0.5 mm wide, densely to sparsely puberulent, usually grouped together on bracteate shoots, the shoot axes up to ca. 2.5 cm long, the bracts scalelike to elliptic, ca. 1–2.5 mm long, caducous at or before anthesis; bracteoles narrowly linear, ca. 1 mm long; calyx lobes linear, linear-oblong, or narrowly triangular with the sides concave, 1–1.5 mm long, the sinuses between the lobes broadly U-shaped; petals suborbicular, ca. 3 mm long; hypanthium obconic, 2–2.5 mm long, not noticeably glan-

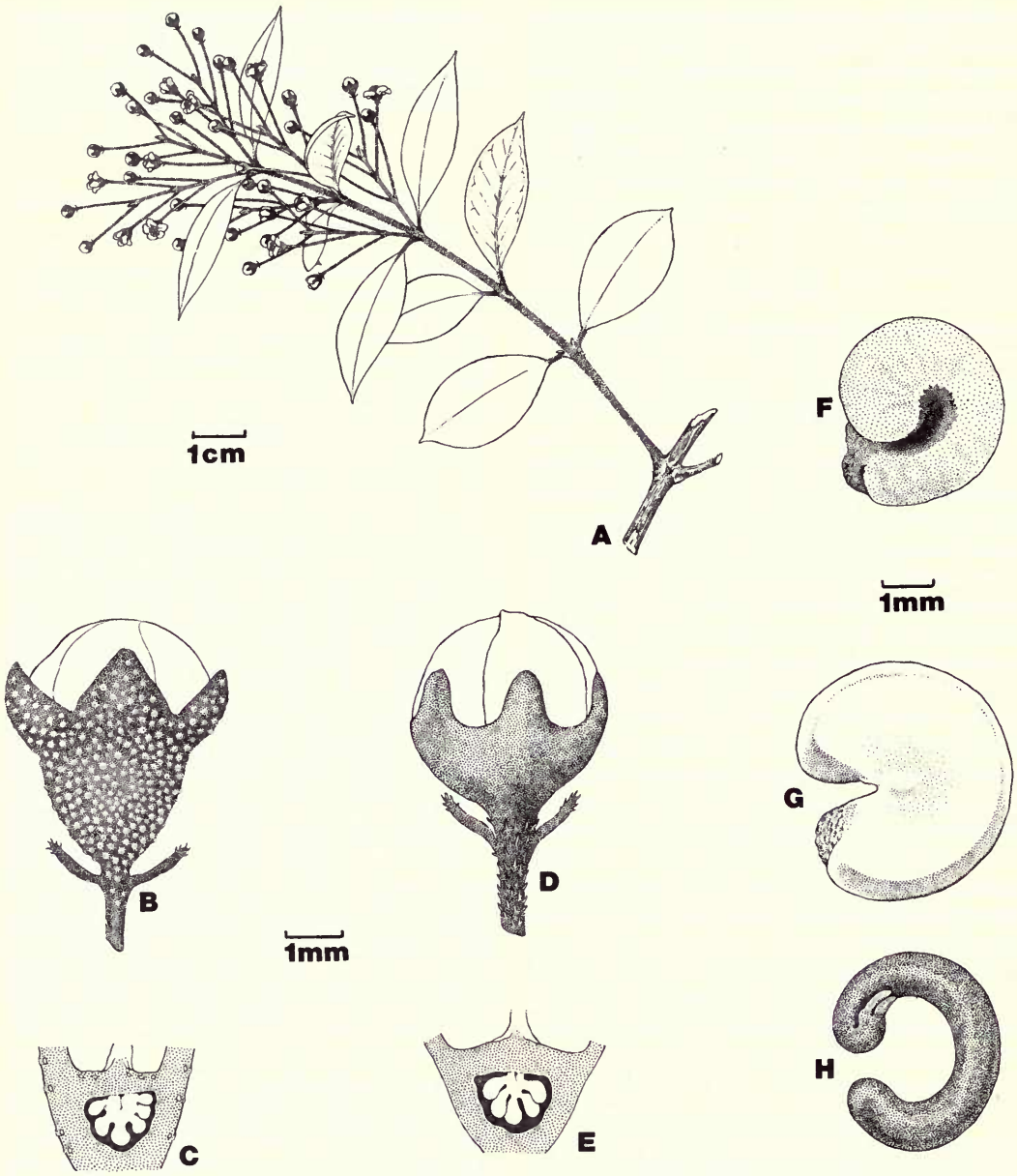


FIGURE 3. *Amomyrtus. Amomyrtus luma* (A, D, E from *Gunckel 1779* at UC; F from *Landrum 3144* at NY): A, twig showing bracteate shoot (raceme) inflorescences. D, bud. E, section of ovary showing placenta and ovules. F, seed. *Amomyrtus meli* (B, C from *Kausel 1434* at F; G, H from *Landrum 3193* at NY): B, bud. C, section of ovary showing placenta and ovules. G, seed. H, embryo. Drawn by Terry Bell.

dular, reddish brown, glabrous or nearly so; disk 2.5–4 mm across, glabrous; style 4–8 mm long, glabrous; stamens ca. 30–45, ca. 4–5 mm long; anthers 0.5 mm long; ovary 2–3-locular; ovules ca. 4–6, the placenta ca. 0.3 mm wide. Fruit black, subglobose, ca. 5–10 mm in diam.; seeds 1–3 per fruit, smooth, hard, grey green, ca. 4–4.5 mm long, the seed coat wall ca. 0.2 mm thick, the embryo purple (Fig. 3A, D–F).

DISTRIBUTION (Fig. 4B).—A tree, usually of wet habitats from Maule to Aisén in Chile and from Neuquén to Chubut in the Andes of Argentina.

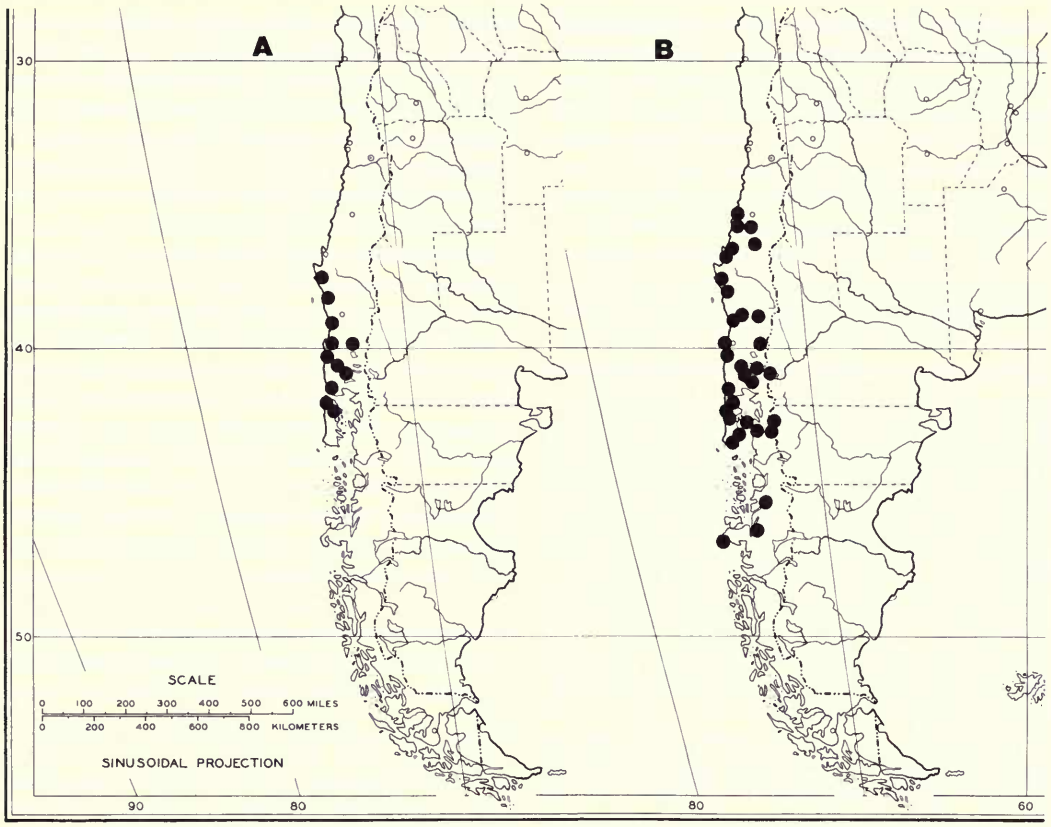


FIGURE 4. Distribution of *Amomyrtus meli* (A) and *A. luma* (B).

PHENOLOGY.—Flowering from September to February, reaching a peak in November. Fruits mainly maturing from February to April.

LOCAL NAMES AND USES.—Luma, palo madroño, cauchao, caochao, cauchahue (Muñoz 1966). *Amomyrtus luma* is said to be used (probably as a leaf tea) as a stimulant and astringent (Muñoz et al. 1981). The fruits are edible and are fermented to make a chicha.

Amomyrtus luma can be distinguished from other species of Chilean Myrtaceae by its reddish brown bark with lighter spots. The bark is not so orange as it is in *Luma apiculata* and *Blepharocalyx cruckshanksii*. *Amomyrtus luma* has strongly aromatic leaves, somewhat less pungent than those of *A. meli*, but with a distinctive fragrance.

3.2. **Amomyrtus meli** (R. A. Philippi) Legrand et Kausel, Lilloa 13:146. ("1947") 1948.

Myrtus meli R. A. Philippi, Linnaea 28:638. 1857.
Pseudocaryophyllus meli (R. A. Philippi) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:515. 1941.

Tree up ca. 20 m high, strongly aromatic, usually only obscurely pubescent on young growth, the trunk with smooth whitish bark, not strongly mottled; hairs whitish, up to ca. 0.3 mm long, usually curved antrorsely; twigs only obscurely pubescent to glabrous, the bark greyish white or light reddish brown, smooth at first, becoming longitudinally broken, longitudinal strips persisting beneath the leaf scars. Leaves ovate, lanceolate, or elliptic, 2–5(–9) cm long, 0.7–2.5(–3) cm wide, 1.4–3.5 times as long as wide; apex acute, often mucronate; base acute; petiole unchanneled to shallowly channeled, 2–4 mm long, 1–2 mm wide, yellowish brown; midvein about flat or slightly raised above, moderately prominent below; lateral veins indistinct or up to ca. 7 pairs faintly visible, the lower pairs ascending, the upper pairs leaving the midvein at an angle of 45 degrees or more; marginal veins about

equalling the laterals in prominence; blades stiffly coriaceous, drying grey green to yellow green, dull to slightly lustrous above. Peduncles solitary (rarely superimposed), 0.4–2 cm long, ca. 0.5 mm wide, glabrous to minutely puberulent, moderately glandular, usually grouped together in bracteate shoots, the bracts caducous before anthesis, elliptic, 1.5–2 mm long; bracteoles linear, ca. 1–1.5 mm long; calyx lobes glabrous, approximately triangular, ca. 1–1.5 mm long, slightly wider than long, the sides nearly straight or slightly concave; petals suborbicular, ca. 3–4 mm long, glabrous, or the margin ciliate; hypanthium obconic, ca. 2.5–3.5 mm long, ca. 3 times as long as the calyx lobes, more or less smooth when dry, densely glandular, the glands noticeable as white spots when dry; disk ca. 4 mm across, glabrous; style 7–8 mm long, glabrous; stamens ca. 40–80, ca. 5–7 mm long; anthers ca. 0.5–0.8 mm long; ovary 2-locular; ovules 5–8 per locule, the placenta ca. 0.5–0.7 mm wide. Fruit black, subglobose, ca. 1–1.5 cm in diam.; seed hard, light colored, smooth, somewhat shiny, ca. 5–6 mm long, the seed coat wall ca. 0.25 mm thick (Fig. 3B, C, G, H).

Distribution (Fig. 4A).—A tree, usually of upland habitats in wet forests from Arauco to Chiloé.

Phenology.—Flowering from October to December but mainly in November. Fruits probably mature mainly from March to May.

Local Name.—Meli.

Amomyrtus meli is usually distinguishable from other Chilean Myrtaceae by its smooth, light bark. The strong aroma of the crushed leaves is distinctive, and once experienced, is easily recognized. The leaves lose most of their aroma upon drying. The fruits are pleasant tasting when ripe.

4. **Blepharocalyx** Berg, Linnaea 27:348 (in key). Jan 1856 ("1854"); 412. Feb 1856.

Temu Berg, Linnaea 30:710. 1861.
Marlieriopsis Kiaerskou, Bot. Tidsskr. 17:281. 1890.
Blepharocalyx subgen. *Temu* (Berg) Niedenzu *in* Engler et Prantl, Nat. Pflanzenfam. 3(7):71. 1893.

Shrubs or trees up to 30 m high; hairs unicellular, simple or symmetrically or asymmetrically dibrachiate, up to ca. 1 mm long. Inflorescence a dichasium of 3 to about 15 flowers in our species; flowers tetramerous, the calyx of 4 separate calyx lobes that persist until the fruit matures in our species; ovary bilocular; ovules aggregated near the center of the septum, aligned in a few irregular rows. Fruit a globose berry; seeds 1–9 in our species, reniform, the testa membranous to cartilaginous; embryo C-shaped in our species, in others reniform, spiral, or nearly straight, the hypocotyl thickened, the cotyledons relatively small, at times scarcely detectable.

Blepharocalyx has three species: *B. cruckshanksii,* an endemic of the forests of southern South America; *B. salicifolius* of southeastern Brazil and along the Andes from Northern Argentina to Colombia; and *B. eggersii* of northern South America and the southeastern Caribbean (Landrum 1986). For many years the Chilean members of the genus have been segregated as the genus *Temu.* I have found that the differences between *B. cruckshanksii* and the other species are minor and thus, I have followed Niedenzu in not accepting *Temu.*

4.1. **Blepharocalyx cruckshanksii** (W. J. Hooker et Arnott) Niedenzu, *in* Engler et Prantl, Nat. Pflanzenfam. 3, Abt. 7:71. 1893.

Eugenia cruckshanksii W. J. Hooker et Arnott, Bot. misc. 3: 321. 1833.
Luma cruckshanksii (W. J. Hooker et Arnott) A. Gray, U.S. Expl. Exped., Phan. 540. 1854.
Eugenia divaricatum Berg, Linnaea 27:257. 1856.
Eugenia divaricatum [var.] α *obovata* Berg, Linnaea 27:257. 1856.
Eugenia divaricatum [var.] β *ovalis* Berg, Linnaea 27:258. 1856.
Eugenia divaricatum [var.] γ *pauciflora* Berg, Linnaea 27:258. 1856.
Temu cruckshanksii (W. J. Hooker et Arnott) Berg, Linnaea 30:711. 1861.
Temu divaricatum (Berg) Berg, Linnaea 30:711. 1861.
Blepharocalyx divaricatus (Berg) Niedenzu, *in* Engler et Prantl, Nat. Pflanzenfam. 3, Abt. 7:71. 1893.
Blepharocalyx divaricatus var. *obovatus* (Berg) Reiche, Anales Univ. Chile 98:707. 1897.
Blepharocalyx divaricatus var. *ovalis* (Berg) Reiche, Anales Univ. Chile 98:707. 1897.
Blepharocalyx divaricatus var. *pauciflorus* (Berg) Reiche, Anales Univ. Chile 98:707. 1897.

Shrub or tree up to 15 m high, the trunk smooth reddish brown; hairs whitish, symmetrically or asymmetrically dibrachiate, up to ca. 0.3(–0.5) mm long; young twigs sparsely pubescent to glabrous, often 4-angled. Leaves elliptic, oblong, elliptic-ovate or elliptic-oblanceolate, 1.7–5.5(–8) cm long, 0.8–3 cm wide, 1.5–2.6 times as long as wide, glabrous or essentially so; apex obtuse or emarginate; base cuneate, acute, acuminate or rounded; petiole slightly channeled, 2–5 mm long,

0.5–1 mm wide, moderately pubescent to glabrous; midvein about flat or slightly raised above, moderately prominent below; lateral veins indistinct or up to ca. 10 pairs moderately distinct; marginal veins equalling the laterals in prominence, looping between them, more or less parallel to the margin; blades submembranous to subcoriaceous, drying grey green, yellowish green, or reddish brown, somewhat darker above than below. Peduncles 1–4.5 cm long, ca. 0.5 mm wide, densely pubescent to glabrous, bearing a dichasium of 3 to ca. 15 flowers, the secondary branches of the dichasium ca. 0.5–1.5 cm long; bracteoles linear, ca. 1.5–2.5 mm long, ca. 0.3 mm wide, caducous at anthesis or before, glabrous to sparsely (rarely densely) pubescent; calyx lobes triangular-ovate, ca. 1–3 mm long and wide, not strongly concave, sparsely (rarely densely) pubescent to glabrous without, sparsely to densely pubescent within; petals suborbicular, ca. 1.5–2.5 mm in diam., sparsely pubescent to glabrous; hypanthium glabrous to sparsely (rarely densely) pubescent, attenuate, funnel-shaped, 2.5–5 mm long; disk ca. 3 mm across, sparsely pubescent to glabrous; stamens ca. 90–140, ca. 5–8 mm long; style ca. 7–8 mm long, glabrous to subglabrous; ovary 2–3-locular; ovules 8–15 per locule. Fruit globose, ca. 7 mm in diam., purple when mature; seeds reniform, ca. 3–4 mm long, 1–9 per fruit, the embryo C-shaped (Fig. 1E–G).

DISTRIBUTION (Fig. 2B).—A small tree of moist, often swampy habitats, endemic to the forests of central and southern Chile from Aconcagua to Llanquihue.

PHENOLOGY.—Flowering mainly from December to February. Fruits maturing from February to April.

LOCAL NAMES.—Temu, palo colorado.

This is one of the most common Myrtaceae in south-central Chile. The bark is often an attractive orange or reddish brown color, as it is in *Luma apiculata* of the same region. The common name temu is applied to both species. The name of a city in southern Chile, Temuco, means "temu water" in the indigenous language, Mapuche.

Flowering specimens of *Blepharocalyx cruckshanksii* are occasionally confused with *Myrceugenia exsucca* because both have well-developed dichasial inflorescences. But, *Blepharocalyx* has deciduous bracteoles, whereas in *Myrceugenia exsucca* they are persistent; in *B. cruckshanksii* the leaf apices are often emarginate, in *M. exsucca* they are not; in *B. cruckshanksii* the hypanthium and twigs are usually only sparsely pubescent and in *M. exsucca* they are usually densely pubescent.

5. **Legrandia** Kausel, Revista Argent. Agron. 9: 321. 1944. *Legrandia* is a monotypic genus endemic to Chile.

5.1. **Legrandia concinna** (R. A. Philippi) Kausel, Revista Argent. Agron. 9:322. 1944.

Eugenia concinna R. A. Philippi, Linnaea 28:640. 1857.

Small tree up to perhaps 8 m high, the young growth sparsely to moderately pubescent; hairs simple, unicellular, whitish, up to ca. 1 mm long; young twigs 4-angled, reddish brown, sparsely to moderately pubescent, with age becoming somewhat rough, grey, subterete, the bark becoming slightly stringy. Leaves elliptic, elliptic-oblong, oval, ovate-elliptic, obovate, 2–5.5 cm long, 0.8–3 cm wide, 1.8–2.8 times as long as wide, glabrous to sparsely pubescent along the midvein and margins, often possessing cavities in the axils of the main lateral veins below, these having ciliate margins; apex obtuse to rounded; base obtuse, cuneate, or acuminate; petiole shallowly channeled, 1–3 mm long, ca. 1 mm thick, glabrous to moderately pubescent; midvein impressed above, prominent below; lateral veins ca. 5–8 pairs moderately prominent, leaving the midvein at an angle of ca. 45 degrees, looping broadly to connect with the succeeding lateral, or splitting about ½–⅔ of the way to the margin, no clear marginal vein present; blades subcoriaceous, drying grey green to reddish brown. Peduncles uniflorous, 1–3.5 cm long, 0.7–2 mm wide, sparsely pubescent to glabrous, solitary in the axils of leaves; bracteoles foliaceous, elliptic, ca. 7–9 mm long, 2–4 mm wide; calyx lobes hemiorbicular-triangular, 3–4 mm long, 4–6 mm wide, glabrous within, sparsely pubescent without; petals 4, suborbicular, to obovate, ca. 7–10 mm long, glabrous except for a ciliate margin; hypanthium obconic to campanulate, 4–7 mm long, densely to moderately pubescent to villose; disk ca. 6 mm across, pubescent centrally, raised conically around the base of the style, the staminal ring glabrous; stamens ca. 200–400, 7–12 mm long; anthers ca. 0.7 mm long; style ca. 9–12 mm long, pubescent basally, otherwise glabrous; ovary 2–3-locular; ovules 5–11 per locule,

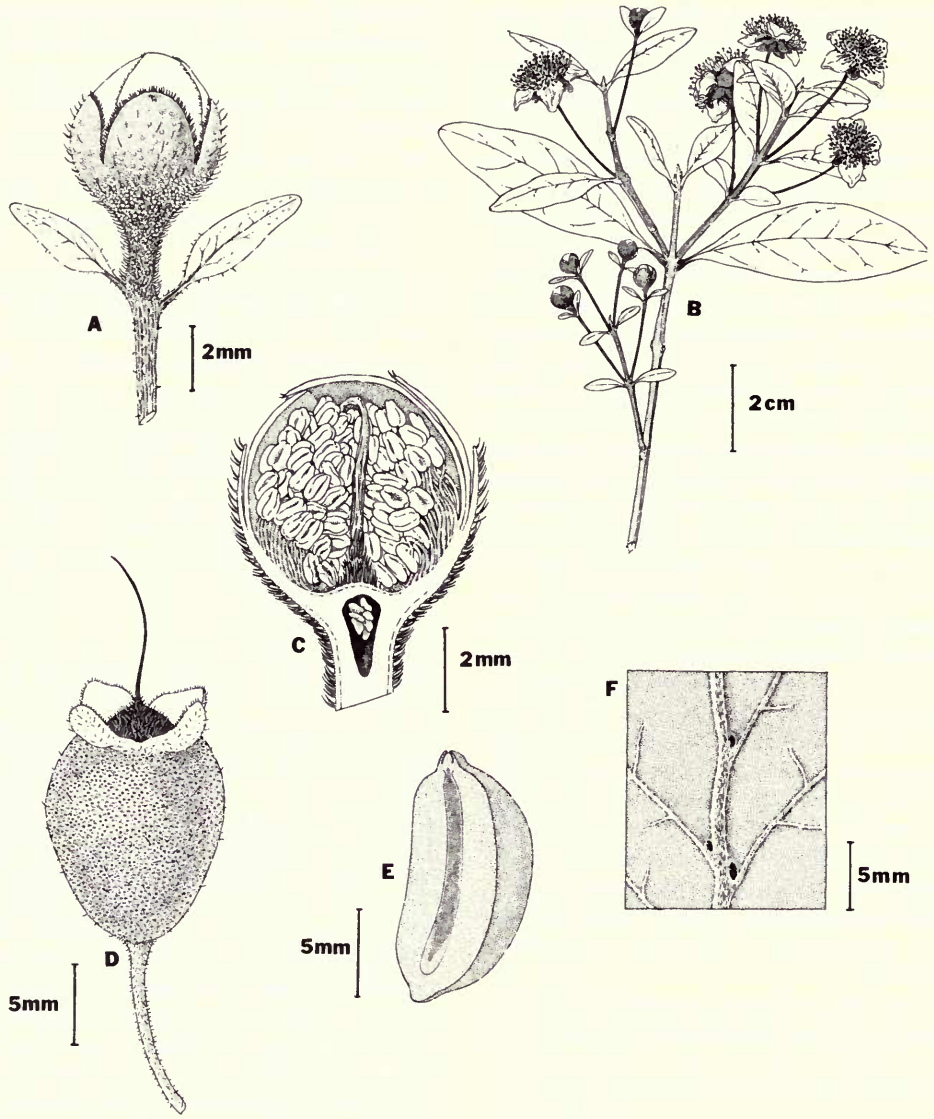


FIGURE 5. *Legrandia concinna* (*Kausel 35* and *Kausel 1516* at F): A, flower with bracteoles attached. B, young branch with flowers. C, longitudinal section of a flower. D, fruit. E, longitudinal section of an embryo. F, lower surface of a leaf showing cavities in the axils of the lateral veins. Drawn by Terry Bell.

more or less biseriate, attached to upper portion of the septum. Fruit subglobose, 1.5–2.5 cm long, drying reddish brown (yellowish when fresh), 1.5–2.5 cm long; seed usually solitary, less often 2–5 per fruit (ex Kausel 1949), the seed coat membranous, the embryo ellipsoidal to subglobose, about straight, ca. 1.3–2 cm long, the central vascular core making up ca. ¼ the diam. of the hypocotyl (Fig. 5).

DISTRIBUTION (Fig. 6).—A smooth-barked tree of wet habitats in the Andes of central Chile from Curicó to Ñuble.

PHENOLOGY.—Flowering is in December and fruits mature in February and March.

LOCAL NAME.—Luma (Kausel 1944). This same name is applied to a few other Chilean species of Myrtaceae, e.g., *Amomyrtus luma.*

Legrandia concinna is readily recognized by its 4-angled young twigs, uniflorous peduncles

FIGURE 6. Distribution of *Legrandia concinna* (triangles) and *Myrteola nummularia* (circles).

bearing relatively large flowers, and foliaceous bracteoles. It is one of the rarest species of Chilean Myrtaceae. The generic name honors Dr. Diego Legrand of Montevideo, Uruguay, an important student of South American Myrtaceae.

6. **Myrteola** Berg, Linnaea 27:393. 1856, nom. cons.

Amyrsia Rafinesque, Sylva tellur. 106. 1838, nom. rejic.
Cluacena Rafinesque, Sylva tellur. 104. 1838, nom. rejic.

Subshrubs or shrubs up to ca. 4 m high; hairs simple, unicellular. Leaves opposite, decussate, often markedly 4-ranked, up to ca. 11 mm long, coriaceous. Inflorescence a solitary flower borne in the axil of a leaf, the peduncles solitary; flowers pentamerous or tetramerous, sometimes both types on a single plant; bracteoles foliaceous, linear to elliptic, persistent; stamens 9–75, the filament mainly longer than the anther during development and at maturity; ovary 2–3-locular, the septum between locules sometimes not complete, the ovules 2–14, biseriate. Fruit a berry ca. 5–8 mm in diam.; seeds 1.2–3 mm long, hard, shiny, smooth, not strongly angular, the seed coat ca. 0.1 mm thick, the inner cavity of the seed C-shaped; embryo C-shaped, the cotyledons nearly as long as the hypocotyl, not folded back against the hypocotyl.

A South American genus of three species of high elevations in the tropical Andes and humid temperate regions (Landrum 1988). *Myrteola* appears to have very close relatives in New Zealand (*Neomyrtus*) and New Caledonia (*Myrtastrum*).

6.1. **Myrteola nummularia** (Poiret) Berg, Linnaea 27:396. 1856.

Myrtus nummularia Poiret *in* Lamarck, Encycl. 407. 1798.
Myrtus nummularia var. *β*, *major* J. D. Hooker, Fl. antarct. 276. 1846.
Myrtus leucomyrtillus Grisebach, Syst. Bemerk. 32. 1854; Abh., Kön. Ges. Wiss. Göttingen 6:120. 1856.
Myrteola bullata Berg, Linnaea 27:394. 1856.
Eugenia humifusa R. A. Philippi, Linnaea 28:639. 1857.
Myrtus repens R. A. Philippi, Bot. Zeitung (Berlin) 15:400. 1857.
Myrteola bullata [var.] *β pentamera* Berg, Bot. Zeitung (Berlin) 15:858. 1857.
Myrteola bullata [var.] *α tetramera* Berg, Bot. Zeitung (Berlin) 15:858. 1857.
Myrteola barneoudii Berg, Linnaea 29:252. 1858.
Myrteola humifusa (R. A. Philippi) Berg, Linnaea 29:252. 1858.
Myrteola repens (R. A. Philippi) Berg, Bot. Zeitung (Berlin) 16:250–251. 1858.
Myrteola leucomyrtillus (Grisebach) Reiche, Anales Univ. Chile 98:702. 1897.
Myrteola barneoudii var. *humifusa* (R. A. Philippi) Reiche, Anales Univ. Chile 98:701. 1897.
Myrteola nummularia var. *repens* (R. A. Philippi) Reiche, Anales Univ. Chile 98:701. 1897.

Creeping subshrub or small shrub up to ca. 1 m high, glabrous or the twigs densely covered with hairs; hairs whitish to reddish brown, simple, up to ca. 0.5 mm long, usually slightly curved, antrorse, appressed or spreading; twigs glabrous to densely pubescent, 4-angled or not, light or dark reddish brown to purplish, with age the bark becoming greyer, exfoliating in longitudinal strips. Leaves elliptic to ovate, 2.5–11 mm long, 1.5–6 mm wide, 1–1.5 times as long as wide, glabrous or with scattered hairs along the margin and midvein, often bullate below because the lower epidermis becomes detached; apex rounded, obtuse, or acute; base rounded to obtuse; petiole 0.5–1.5 mm long, ca. 0.5–0.8 mm wide glabrous or moderately pubescent; midvein impressed or about flat above, noticeable to indistinct below; lateral and marginal veins indistinct; blades coriaceous, shiny above, often dotted with glands above, drying grey green, or tinged with red. Peduncles ca. 1–9 mm long, ca. 0.3 mm wide, glabrous to pubescent, the epidermis wrinkled longitudinally or not; bracteoles foliaceous, glabrous to subglabrous, linear to elliptic, often persisting until fruit matures, 1.5–3.5 mm long, 0.5–1.5 mm wide; calyx lobes 4 or 5, linear-oblong to hemielliptic, 1.2–2.5 mm long, 0.6–1 mm wide, glabrous to subglabrous; petals 4 or 5, elliptic to obovate, ca. 3–4 mm long, white or tinged with pink, glabrous or the margin ciliate; hypanthium narrowly campanulate, 2–3 mm long, usually about 1.5 times as long as calyx lobes, glabrous to pubescent; disk ca. 2 mm across, glabrous to pubescent; style 3–4 mm long, glabrous, the stigma more or less dilated, ca. 0.2 mm wide; stamens 9–18, 4–5 mm long; anthers 0.2–0.3 mm long; ovary 2–3-locular; ovules (2–)6–12(–14) per locule. Fruit subglobose, reddish to white, tinged with pink; seeds usually several, reniform, shiny, 1.2–1.5 mm long; 2n = 44 (Moore 1983) (Fig. 7).

Distribution (Fig. 6).—A shrub or subshrub of *Sphagnum* bogs and other wet habitats from about 1,300 m to about sea level in south-central and southern Chile and adjacent Argentina to the tip of South America; and on the Masafuera of the Juan Fernández Islands and on the Falkland Islands. This species also grows in paramos at elevations of 2,500–3,700 m in the Andes of Venezuela, Colombia, Ecuador, Peru, and Bolivia. Various synonyms proposed for populations of northern South America are not listed here but can be consulted in my revision of *Myrteola* (Landrum 1988).

Phenology.—Flowering mainly from November to February; fruiting mainly in February and March.

Local Names and Uses.—Daudapo, huarapo, naurapo (Muñoz 1966). The fruits are edible.

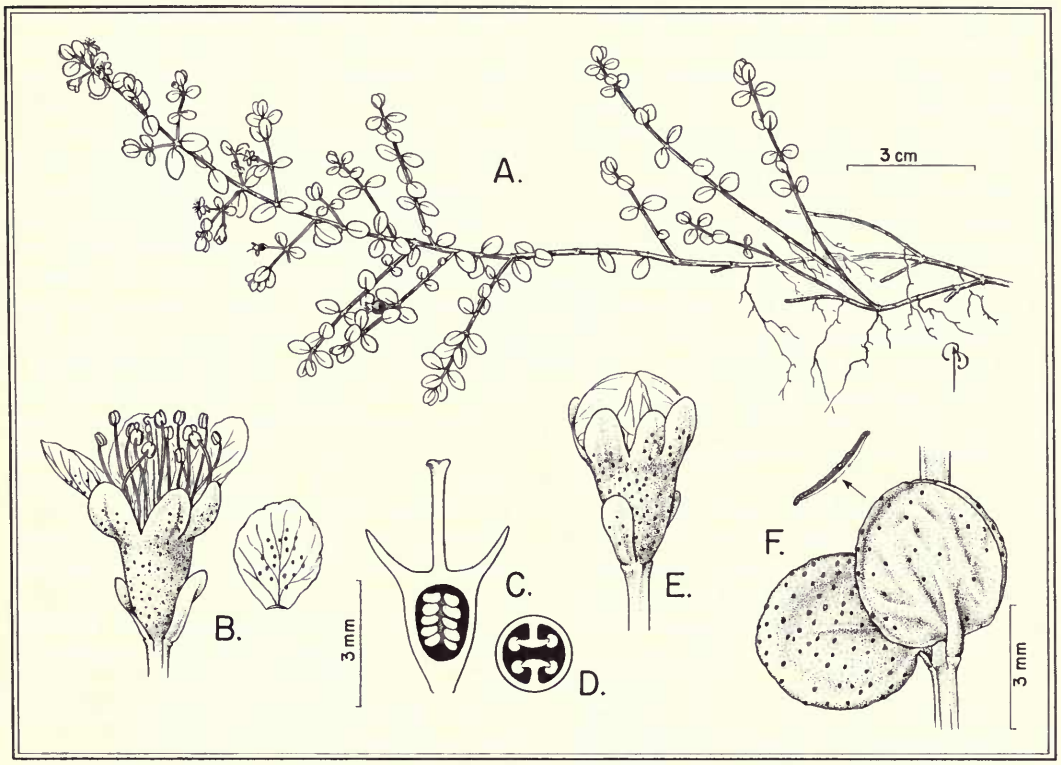


FIGURE 7. *Myrteola nummularia* (*Werdermann 275* at CAS). A, habit. B, open flower and petal. C, longitudinal section of ovary. D, cross section of ovary showing incompletely fused locules. E, flower bud. F, leaves showing detached lower epidermis. Drawn by Bobbi Angell.

Myrteola nummularia is distinguished by its usually creeping habit, small leaves usually less than 1 cm long, the lower epidermis of which often becomes detached, persistent bracteoles, and small berry fruits. It is probably most likely to be confused with *Ugni* from which it differs in having erect flowers and exserted stamens.

7. **Ugni** Turczaninow, Bull. Soc. Imp. Naturalistes Moscou 21:579. 1848; Flora 31:711. 1848.

Shrubs up ca. 3 m high; hairs unicellular, simple or dibrachiate. Leaves opposite, persistent, coriaceous, mainly elliptic to lanceolate. Inflorescence a solitary, nodding flower, the peduncles not superimposed, borne in the axils of leaves or bracts; flowers usually pentamerous, less often both pentamerous and tetramerous on a single plant, the corolla campanulate, the stamens not exceeding the corolla, the filaments short, the anthers elongate, more or less sagitate, introrsely dehiscent; bracteoles persistent usually until the fruit matures, linear to narrowly elliptic; ovary usually 3(–4)-locular, the ovules biseriate, 4-seriate, or multiseriate. Fruit a berry, the seeds few to many, shiny light brown, small, ca. 1–2 mm long; embryo C-shaped, the cotyledons almost as long as the hypocotyl, scarcely if at all folded back against themselves.

Ugni is distinguished from other genera of Chilean Myrtaceae by nodding flowers with the stamens shorter than the petals and introrsely dehiscent anthers. In fruit it is distinguished from all but *Myrteola nummularia* by having persistent bracteoles and very small (1–2 mm long), hard seeds. *Myrteola nummularia* differs in having a usually creeping habit, small leaves usually no more than 1 cm long, and a lower leaf epidermis that often becomes detached.

KEY TO THE SPECIES OF *UGNI*

1. Young twigs densely covered with reddish brown, asymmetrically dibrachiate hairs; calyx lobes hemiorbicular-triangular, about

as long as wide, the sides convex in outline; midvein raised or flat above; stamens usually more than 60; ovules biseriate; continental Chile ..... 7.1. *U. candollei*

1. Young twigs densely to sparsely covered with whitish (rarely reddish brown), unbranched hairs; calyx lobes narrowly triangular to linear, normally longer than wide, the sides concave in outline; midvein usually impressed above; stamens usually less than 60; ovules biseriate to multiseriate
   2. Bracteoles spreading to ascending; leaves strongly glandular-punctate, thick, fleshy; leaf apex obtuse to rounded; petiole more or less flat, 1–1.5 mm wide; Masatierra, Juan Fernández ..... 7.3. *U. selkirkii*
   2. Bracteoles reflexed; leaves usually not strongly glandular-punctate, nor thick, nor fleshy; leaf apex acute to acuminate; petiole usually channeled, 0.3–ca. 1 mm wide; continental and introduced to Juan Fernández and growing in disturbed sites ..... 7.2. *U. molinae*

7.1. **Ugni candollei** (Barnéoud) Berg, Linnaea 27: 388. 1856.

Myrtus candollei Barnéoud, *in* Gay, Fl. Chil. 2:382. 1847.
Myrtus krausei R. A. Philippi, Linnaea 28:638. 1857.
Ugni krausei (R. A. Philippi) Berg, Bot. Zeitung (Berlin) 16: 250. 1858.
Ugni candollei forma *litoralis* Kausel, Lilloa 17:54. 1949.
Ugni candollei forma *monticola* Kausel, Lilloa 17:54. 1949.

Shrub up to ca. 2 m high; usually rusty brown pubescent on twigs and young growth; hairs asymmetrically dibrachiate to nearly simple, up to ca. 1 mm long, rusty brown or less often whitish, the longer arm directed antrorsely; twigs moderately to densely pubescent when young, the hairs sometimes appearing to be in tufts, often obscuring the light reddish brown bark, the older twigs becoming grey, with rough, stringy, or flaky bark. Leaves elliptic, ovate, lanceolate, obovate, or oblanceolate, 1–3 cm long, 0.4–1.7 cm wide, 1.5–3 times as long as wide, sparsely to moderately pubescent, more densely so along the midvein; apex acute to acuminate; base acute to rounded; petiole 1–3 mm long, ca. 0.5–0.8 mm wide, about flat above, sparsely to densely pubescent; midvein flat or raised slightly above, prominent to only visible below; lateral veins indistinct or about 10 pairs faintly visible; marginal veins equalling the laterals in prominence; blades stiffly coriaceous, drying light grey green to reddish brown, somewhat darker above than below. Peduncles 0.5–3.5 cm long, ca. 0.5 mm wide, sparsely to densely pubescent; bracteoles narrowly elliptic to linear; calyx lobes ovate-triangular to ovate-hemiorbicular, the apex often acuminate, sparsely pubescent to glabrous without, glabrous within; petals suborbicular, 6–9 mm long, white, membranous, glabrous; hypanthium obconic to campanulate, 2–3.5 mm long, densely to sparsely pubescent; disk ca. 3 mm across, glabrous; style 3–6 mm long, glabrous; stamens 50–120, 2–3 mm long, the lanceolate, apiculate anther about ½ the length; ovary 3-locular; ovules 11–20 per locule, biseriate. Fruit subglobose, up to ca. 1 cm in diam., reddish to black; seeds numerous to few, ca. 2 mm long, the pulp of the fruit clinging to the seeds (Fig. 8A–D).

Distribution (Fig. 9A).—A shrub of moist habitats. Known from Maule, and from Valdivia to Chiloé.

Phenology.—Flowering mainly in January and February; fruiting mainly from February to April.

Local Names.—Murta, murta blanca, tautau, chauchau, trautrau (Muñoz 1966).

Ugni candollei is the only species of the genus with reddish brown dibrachiate hairs. The calyx lobes are usually about as long as wide, whereas in other species they are longer than broad. The only species with which it could be confused is *Ugni molinae. Ugni candollei* seems to be somewhat more tolerant of cool wet climates than *U. molinae,* growing either at high elevations (e.g., in the Cordillera Pelada) or farther south. The corollas of *U. candollei* seem to be somewhat more broadly campanulate than those of *U. molinae.*

The fruits of *U. candollei* are not as delicious as those of *U. molinae,* but it is an attractive shrub that would have horticultural value.

7.2. **Ugni molinae** Turczaninow, Bull. Soc. Imp. Naturalistes Moscou 21:579. 1848; Flora 31: 711. 1848.

Myrtus ugni Molina, Sag. stor. nat. Chili, ed. 1, 161. 1782.
Eugenia ugni (Molina) W. J. Hooker et Arnott, Bot. misc. 3: 318. 1833.
Ugni poeppigii Berg, Linnaea 27:386. 1856.
Ugni philipii Berg, Linnaea 27:387. 1856.
Ugni ugni (Molina) Macloskie, Rep. Princeton Univ. Exped. Patagonia, Botany 8:602. 1905.
Ugni myrtus Macloskie, Torreya 5:198. 1905.

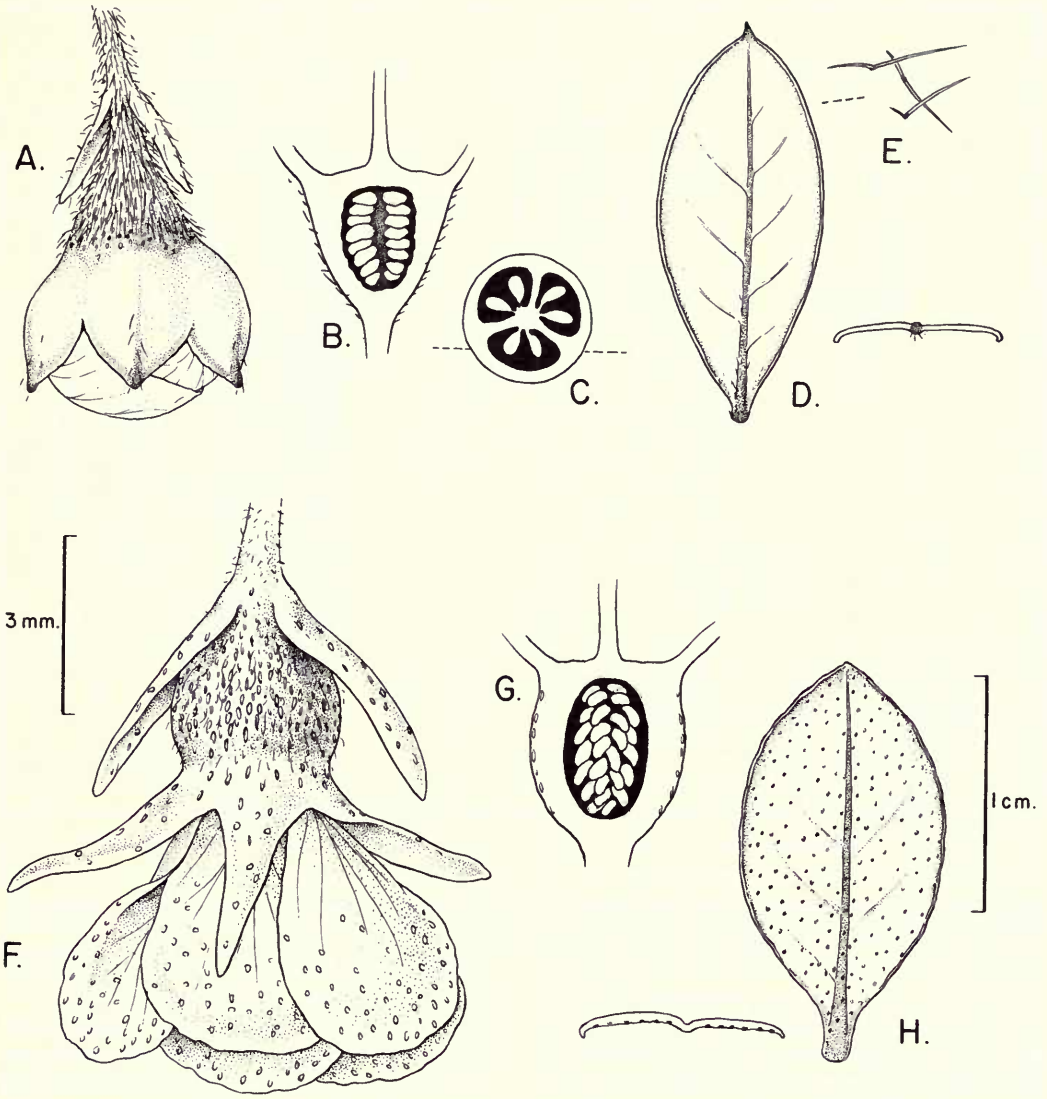


FIGURE 8. *Ugni. Ugni candollei* (*Eyerdam 10589* at NY): A, bud. B, longitudinal section of ovary. C, cross section of ovary. D, lower leaf surface and section of leaf showing raised midvein. E, magnified view of dibrachiate hairs. *Ugni selkirkii* (*Skottsberg 333* at NY): F, opening flower. G, longitudinal section of an ovary. H, lower surface of leaf and section of leaf showing impressed midvein.

Shrub up to ca. 2 m high, obscurely whitish pubescent on twigs and young growth; hairs simple, whitish, up to ca. 0.5 mm long, straight or curved, directed antrorsely; twigs sparsely to moderately pubescent when young, glabrescent with age, the young bark at first light reddish brown, smooth, becoming yellowish brown to grey, flaky, stringy, or nearly smooth. Leaves ovate, lanceolate, or elliptic, 1.4–3.6 cm long, 0.8–2 cm wide, 1.5–3 times as long as wide, glabrous or with a few scattered hairs below; apex acute to acuminate; base acute to broadly rounded; petiole shallowly channeled, 2–4 mm long, ca. 1 mm wide, sparsely pubescent to glabrous; midvein impressed above, prominent below; lateral veins indistinct or a few pairs faintly visible; marginal veins equalling laterals in prominence; blades stiffly coriaceous, not strongly glandular, drying dark green to reddish brown above, much lighter yellow green below, the margins usually

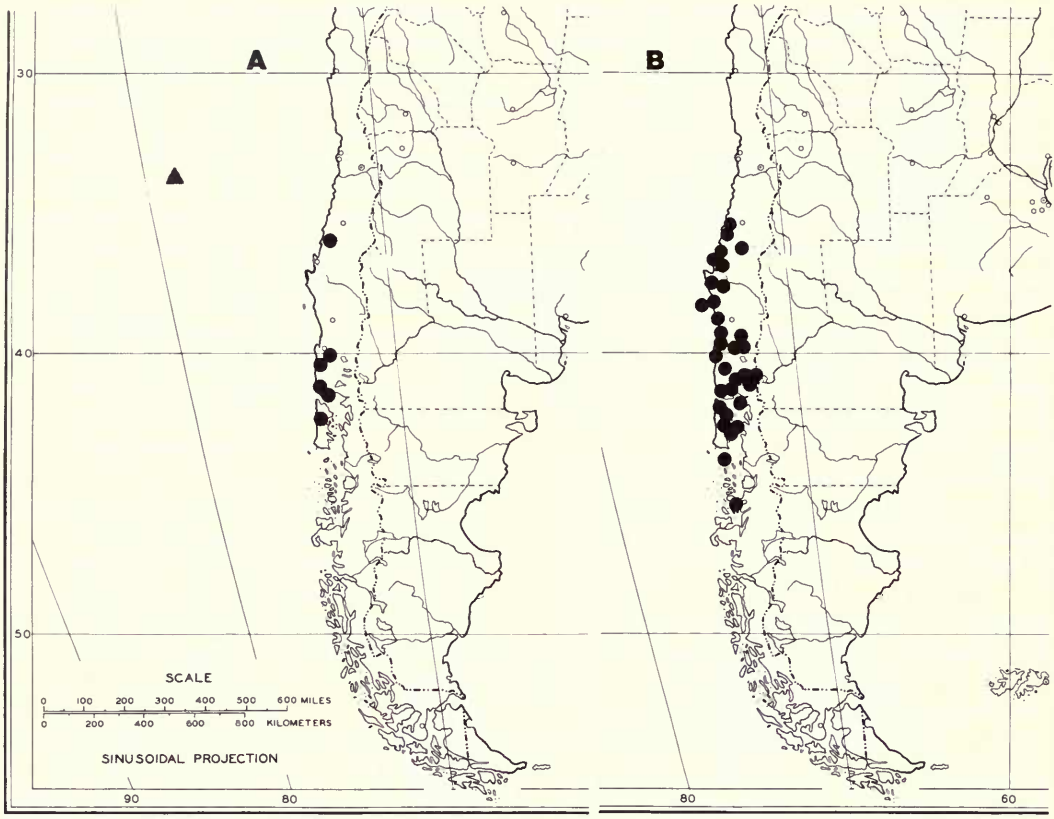


FIGURE 9. Distribution of *Ugni candollei* (A, circles), *U. selkirkii* (A, triangles), and *U. molinae* (B, circles).

slightly revolute. Peduncles 1–2.5 cm long, ca. 0.5–0.8 mm wide, normally glabrous to very sparsely pubescent, borne in the axils of leaves or bracts ca. 1–3 mm long; bracteoles linear to narrowly elliptic, 5–8 mm long, 0.5–1.5 mm wide, glabrous to very sparsely pubescent, reflexed; calyx lobes triangular, triangular-lanceolate, triangular-linear, or narrowly attenuate-triangular, 2–5 mm long, 1–2.5 mm wide, glabrous to very sparsely pubescent, the margins concave in outline; petals suborbicular, fleshy, 5–8 mm long, ca. 0.3–0.4 mm thick at base, pink when fresh, drying brown with light margins, veins not clearly visible; hypanthium subglobose to campanulate, ca. 2–3 mm long, glabrous to very sparsely pubescent; disk 2–4 mm across, glabrous; style 4–5 mm long, glabrous; stamens 40–60, 2–4 mm long, the ovate, lanceolate, or obovate anthers ca. 1–1.5 mm long, the filament flattened, ca. 0.3–0.8 mm wide; ovary 3-locular; ovules per locule 13–30, usually 4-seriate. Fruit subglobose, ca. 1 cm in diam., dark red; seeds 1.5–2 mm long, smooth; 2n = 22 (Sanders et al. 1983) (Fig. 10).

DISTRIBUTION (Fig. 9B).—A shrub of relatively dry to wet habitats from Linares and Maule to Chiloé in Chile, and Lago Nahuel Huapi (on the border of Río Negro and Neuquén) in Argentina.

PHENOLOGY.—Flowering mainly from December to February; fruits ripening mainly February–April.

LOCAL NAMES AND USES.—Uñi, murta, murtilla, murtillo (Muñoz 1966). The fruits of *Ugni molinae* are very delicious and commonly gathered from the wild to make marmalades and liqueurs. It is sometimes cultivated in California as an ornamental.

Ugni molinae might be confused with *U. candollei* on the continent and the differences are discussed under that species. On Masatierra it has been introduced, and there it has been mistaken for *U. selkirkii*. The two are compared directly in the key, but it is worth noting that *U.*

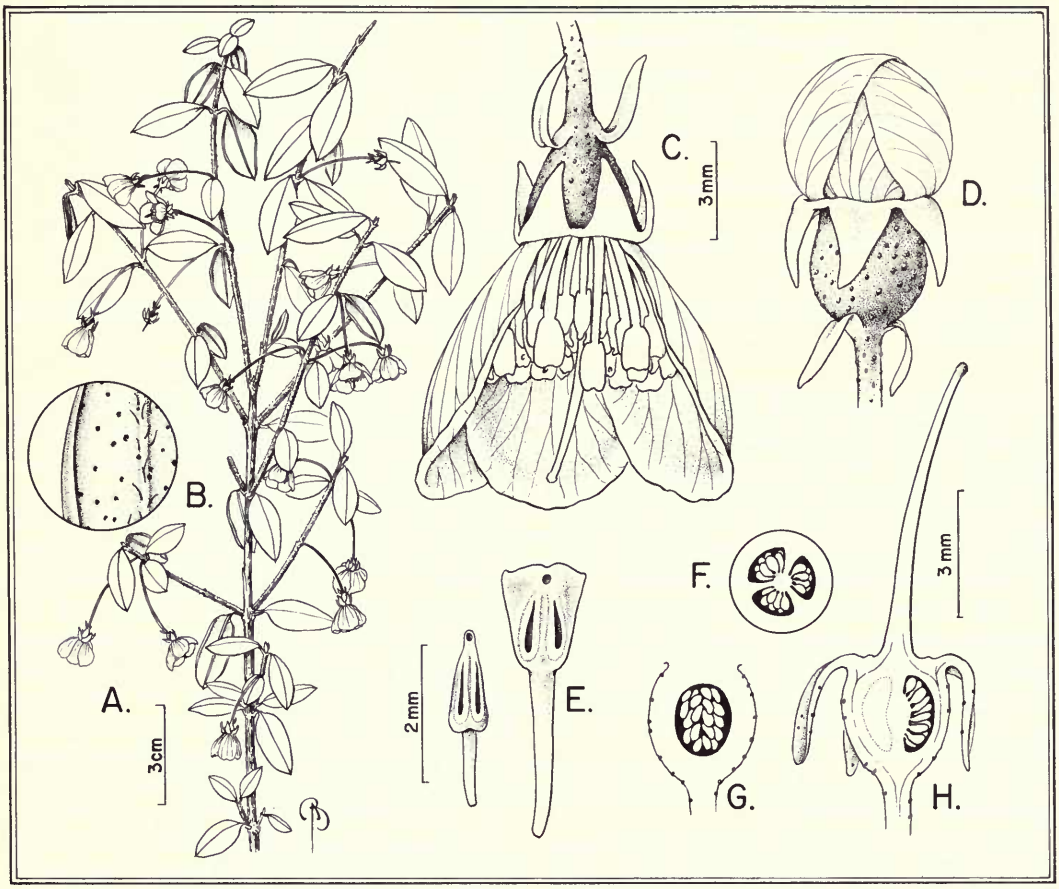


FIGURE 10. *Ugni molinae* (*Werdermann 306* at CAS). A, habit. B, insert of lower leaf surface. C, open flower with two petals removed. D, flower bud. E, stamens showing anthers with terminal glands and introrsely directed slits. F, cross section of ovary. G, longitudinal section of ovary with ¼ cut away. H, longitudinal section through old flower.

molinae is a weedy species of disturbed sites on the island, whereas *U. selkirkii* grows in undisturbed areas, usually at higher elevations.

7.3. **Ugni selkirkii** (W. J. Hooker et Arnott) Berg, Linnaea 27:392. 1856.

Eugenia selkirkii W. J. Hooker et Arnott, Bot. misc. 3:318. 1833.

Myrtus berteroi R. A. Philippi, Bot. Zeitung (Berlin) 14:644. 1856.

Ugni berteroi (R. A. Philippi) F. Philippi, Cat. pl. vasc. chil. 79. 1881.

Shrub up to ca. 3 m high, obscurely whitish pubescent on twigs and young growth; hairs simple, whitish, up to ca. 0.5 mm long, usually straight, more or less appressed, usually antrorsely directed; twigs sparsely to densely pubescent when young, glabrescent with age, the young bark at first light reddish brown, smooth, becoming grey, scaly or rough. Leaves elliptic, suborbicular, or obovate, 0.8–2.2 cm long, 0.7–1.4 cm wide, 1.2–2(–2.3) times as long as wide, glabrous or sparsely pubescent; apex obtuse to rounded; base acuminate, acute, or rounded; petiole nearly flat above, 2–3 mm long, 1–1.5 mm wide, glabrous to sparsely pubescent; midvein impressed above, moderately prominent below; lateral and marginal veins indistinct to faintly visible; blades thickly coriaceous (probably somewhat fleshy when fresh), strongly glandular, drying dark grey green to reddish brown above, lighter yellow green or tan below, the margin revolute. Peduncles 0.7–1.5 cm long, ca. 0.8–1 mm wide, sparsely to moderately pubescent; bracteoles more or less linear, 4–7 mm long, ca. 0.8–1 mm wide, spreading or ascending, not reflexed, glabrous to sparsely pu-

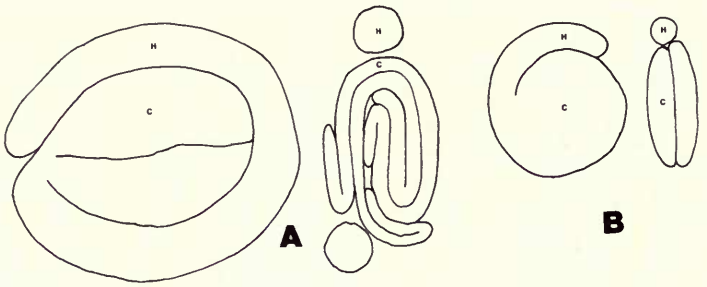


FIGURE 11. Embryos of *Myrceugenia* (A) and *Luma* (B), side views on left and sections on right. Small c = cotyledon, small h = hypocotyl.

bescent; calyx lobes oblong to linear (rarely triangular), usually with a broadened base, 2.5–4.5 mm long, 1.5–3 mm wide at base, glabrous within, glabrous to sparsely pubescent without; petals suborbicular to obovate, 4–5 mm long, glabrous, glandular; hypanthium campanulate to globose, ca. 4 mm long, sparsely pubescent; disk ca. 1.5–2.5 mm across, glabrous; style ca. 4 mm long, glabrous; stamens 30–40, 1.5–3 mm long, the anther ca. 1 mm long; ovary 3(–4)-locular; ovules 23–41 per locule, multiseriate. Fruit subglobose, ca. 1 cm in diam.; seeds ca. 1 mm long; 2n = 44 (Sanders et al. 1983) (Fig. 8F–H).

DISTRIBUTION (Fig. 9A).—Known only from Masatierra, Juan Fernández.

PHENOLOGY.—Flowering mainly from January to March; fruits probably ripening in April and May.

Ugni selkirkii might only be confused with *U. molinae*. They are compared directly in the key and in the discussion of that species.

Myrciinae Berg, 1855

8. **Myrceugenia** Berg, Linnaea 27:5 (in key). 1855; Linnaea 27:131. 1856.

Myrcia subgen. *Myrceugenia* (Berg) Kiaerskou, Enum. Myrt. bras. 115. 1893.
Nothomyrcia Kausel, Lilloa 13:148. 1948 ("1947").

Trees to ca. 10 m high or much-branched shrubs less than 1 m high; hairs simple or dibrachiate, unicellular. Leaves opposite (rarely ternate or subopposite), variously shaped, usually not strongly aromatic. Inflorescence axillary, uniflorous or a dichasium with 1–3 levels of bifurcation, the peduncles borne in the axils of leaves or small bracts, solitary or superimposed in rows of 2–4, the lateral branches of the dichasia often superimposed; bracteoles normally persisting until the fruit matures, rarely (in *M. fernandeziana*) caducous at anthesis; ovary 2–4-locular, the ovules 2 to about 20 per locule, biseriate. Fruit a berry, yellow, orange, reddish, or dark purple, the seeds usually 1–5, the testa membranous; embryo globose, the cotyledons thin, membranous, folded into a bundle, the hypocotyl about as long as the cotyledons, horseshoe-shaped, encircling the cotyledons (Fig. 11A); 2n = 22 (Landrum 1981; Sanders et al. 1983).

Myrceugenia can be distinguished from other genera of Chilean Myrtaceae when in fruit by its embryo and usually when in flower by its combination of tetramerous flowers and persistent, reduced, clasping bracteoles. *Myrceugenia obtusa* has foliaceous bracteoles, and *M. fernandeziana* has bracteoles that are caducous at anthesis.

There are 40 species of *Myrceugenia* (Landrum 1981, 1984), 14 of which grow in Chile and adjacent Argentina. The rest grow in southeastern Brazil, Paraguay, Uruguay, and northeastern Argentina. *Myrceugenia ovata* has varieties in both eastern and western South America.

Local names for species of *Myrceugenia* are probably not consistently applied in Chile except for the more easily recognized species, but luma, arrayán, peta, pitra, petra, and diminutives of these are often used.

KEY TO THE SPECIES OF *MYRCEUGENIA*

1. Bracteoles scarious, caducous at anthesis; hairs simple; midvein not impressed; Masatierra, Juan Fernández ..... 8.5. *M. fernandeziana*

1. Bracteoles not scarious, not caducous at anthesis, usually persisting until the fruit matures; at least some hairs dibrachiate; midvein usually impressed; not on Masatierra
   2. Leaves less than 2 cm long, ca. 0.2–0.5 mm wide, densely covered with reddish brown appressed dibrachiate hairs beneath; coastal shrub of central Chile ..... 8.13. *M. rufa*
   2. Leaves larger and/or not covered with reddish brown dibrachiate hairs beneath
      3. Dichasial inflorescences present
         4. Twigs and flowers yellowish lanate; Masafuera, Juan Fernández ..... 8.14. *M. schulzei*
         4. Twigs and flowers not yellowish lanate; mainland
            5. Leaves 1–2.5 times as long as wide; dichasia usually with more than 3 flowers; twigs not reddish; bracteoles usually less than 0.5 mm wide ..... 8.4. *M. exsucca*
            5. Leaves 3–15 times as long as wide; dichasia usually with no more than 3 flowers; twigs reddish; bracteoles usually 0.5–1 mm wide ..... 8.6. *M. lanceolata*
      3. Dichasial inflorescences not present
         6. Bracteoles leaflike, petiolate, linear, oblong, elliptic, or spatulate, 2–6 mm long, 0.5–2.5 mm wide, not clasping the hypanthium; leaf apex blunt, obtuse, or rounded
            7. Hypanthium 1–2 mm long; peduncles solitary, 0.4–0.6 mm wide; hairs a mixture of simple and dibrachiate; leaf margins not revolute ..... 8.8. *M. obtusa*
            7. Hypanthium 2.5–4 mm long; peduncles often in pairs, 1–1.5 mm wide; hairs all symmetrically dibrachiate; leaf margins revolute ..... 8.3. *M. correifolia*
         6. Bracteoles not leaflike, generally ovate to lanceolate, clasping the hypanthium; leaf apex usually acute
            8. Peduncles glabrous or with only scattered hairs
               9. Twigs densely pubescent; leaves 1–2.6 cm long, 0.3–0.7 cm wide; peduncles solitary; lower elevations ..... 8.10. *M. parvifolia*
               9. Twigs glabrous or nearly so; leaves 1.3–5 cm long, 0.5–2.5 cm wide; peduncles often in pairs; mainly above 700 m ..... 8.1. *M. chrysocarpa*
            8. Peduncles pubescent, the hairs sometimes very small
               10. Leaves linear, narrowly oblong, or oblanceolate, mainly 3–15 times as long as wide
                  11. Leaves oblanceolate to linear; twigs reddish; hypanthium 1.5–2 times as long as wide, usually slightly contracted just below the calyx lobes ..... 8.6. *M. lanceolata*
                  11. Leaves elliptic to linear; twigs not reddish; hypanthium usually about as wide as or wider than long, not contracted just below the calyx lobes
                     12. Hypanthium 1.5–2 mm long; leaves strongly discolorous, dark green above, light green below; stamens about 100–150; calyx lobes about as long as or shorter than the hypanthium ..... 8.11. *M. pinifolia*
                     12. Hypanthium about 1 mm long or shorter; leaves more or less concolorous, light grey green; stamens about 60–100; calyx lobes about 1.5 times as long as the hypanthium ..... 8.7. *M. leptospermoides*
               10. Leaves usually elliptic, ovate, obovate, or oblong, mainly less than 3 times as long as wide
                  13. Twigs and flowers yellowish lanate; essentially all hairs symmetrically dibrachiate
                     14. Leaves mainly 1–2 cm long (shade leaves occasionally longer), often verticillate, the apex broadly rounded; calyx lobes not greenish, coriaceous, more or less acute; mainland ..... 8.2. *M. colchaguensis*
                     14. Leaves 1.5–5(–6) cm long, some normally well over 2 cm long, not verticillate, the apex often acute or acuminate; calyx lobes greenish, rounded or blunt, membranous; Masafuera, Juan Fernández ..... 8.14. *M. schulzei*
                  13. Twigs and flowers not yellowish lanate; hairs symmetrically dibrachiate or not

15. Peduncles densely covered with reddish brown hairs
    16. Leaves mainly 1–3 cm long; hairs a mixture of simple and asymmetrically dibrachiate; leaf margins not revolute; bracteoles 0.5–2 mm long; coast and interior from Linares to Chiloé ..... 8.9. *M. ovata*
    16. Leaves often exceeding 3 cm long; hairs appressed, all symmetrically dibrachiate; leaf margins strongly revolute; bracteoles 3–8 mm long; coast from Curicó to Coquimbo ..... 8.3. *M. correifolia*
15. Peduncles sparsely pubescent or if densely pubescent, the hairs whitish
    17. Hypanthium (1.5–)2–4 mm long, densely covered with minute appressed, whitish hairs; peduncles ca. 1 mm wide, usually densely glandular; leaves almost all acuminate at both apex and base, mainly 3–8 cm long; generally at altitudes below 700 m ..... 8.12. *M. planipes*
    17. Hypanthium 1–2 mm long, glabrous to densely pubescent, the hairs whitish, yellowish, or reddish brown; peduncles 0.5–1 mm wide, with few or no glands; leaves often rounded or blunt at apex or base, often all under 3 cm long; generally at altitudes of 700–1,000 m ..... 8.1. *M. chrysocarpa*

8.1. **Myrceugenia chrysocarpa** (Berg) Kausel, Revisión de las Mirtáceas Chilenas 2. 1940; Revista Argent. Agron. 9:58. 1942.

Eugenia chrysocarpa Berg, Linnaea 27:168. 1856.
Eugenia philippi Berg, Linnaea 27:145. 1856.
Eugenia buxifolia R. A. Philippi, Linnaea 28:640. 1857.
Eugenia patagonica R. A. Philippi, Linnaea 33:72. 1864.
Eugenia petiolata R. A. Philippi, Anales Univ. Chile 84:757. 1893.
Myrceugenia buxifolia (R. A. Philippi) Reiche, Anales Univ. Chile 98:712. 1897; Fl. Chile 2:296. 1898.
Luma chrysocarpa (Berg) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:524. 1941.
Luma philippi (Berg) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:523. 1941.

Shrub up to ca. 3 m high, without glands or at least not conspicuously glandular; hairs reddish brown to whitish, mainly appressed, dibrachiate; twigs moderately pubescent to glabrous when young, soon glabrescent. Leaves glabrous or with a few scattered, inconspicuous hairs, usually elliptic, ovate, or lanceolate, less often obovate or oblanceolate, 1.3–5(–6) cm long, 0.5–2.5 cm wide, 1.5–4.5(–5.8) times as long as wide; apex acute, obtuse, or rounded; base obtuse, acute, or cuneate; petiole channeled, 3–6 mm long, 0.5–1 mm thick, glabrous to very sparsely pubescent; midvein impressed for entire length or nearly so above, moderately prominent below, at least proximally; lateral veins indistinct or up to ca. 15 pairs faintly visible; marginal veins equalling laterals in prominence; blades coriaceous, light grey green, yellow green to somewhat olive green above, light grey green or yellow green below, often concolorous, both surfaces dull. Peduncles uniflorous, flattened, 3–16 mm long, 0.6–1 mm wide, glabrous to sparsely pubescent, solitary or in pairs in the leaf axils; bracteoles lanceolate, 1.3–2.7 mm long, 0.6–1.4 mm wide, 1.9–2.7 times as long as wide, coriaceous, clasping the hypanthium, glabrous within, glabrous or with scattered hairs without; calyx lobes ovate to ovate-oblong, 1.7–3.2 mm long, 1.5–3.4 mm wide, 0.8–1.4 times as long as wide, subcoriaceous, glabrous to very inconspicuously and sparsely pubescent within and without, concave; petals glabrous, white to tan when dry, suborbicular, 2–4 mm in diam.; hypanthium obconic, the walls often sightly concave, 1.3–2 mm long, densely pubescent to nearly glabrous; disk 2–3 mm across, glabrous or with occasional hairs; stamens 70–150, 3–10 mm long; anthers slightly elongate, 0.3–0.5 mm long; style glabrous, 7–10 mm long; ovary 2–3-locular; ovules 3–10 per locule. Fruit globose, 7–12 mm in diam., orange brown; seeds 1–5 in fruits seen, oblong, ca. 4–5 mm long (Fig. 12H).

Distribution (Fig. 13A).—In mountainous areas, usually above 700 m, usually in forests of *Nothofagus dombeyi,* from Malleco to Chiloé in Chile and in the Andes of Neuquén, Río Negro, and Chubut in Argentina.

Phenology.—Flowering in February and

March. Fruits mature from November to February.

Myrceugenia chrysocarpa is distinguished by leaves that are essentially glabrous and concolorous. Peduncles that are glabrous or sparsely pubescent, uniflorous and often superimposed; and a mountainous habitat, usually above 700 m. It is probably the most cold-tolerant species of Myrtaceae in Chile. It is occasionally confused with *M. planipes,* with which it is compared directly in lead 17 of the key.

8.2. **Myrceugenia colchaguensis** (R. A. Philippi) Navas, Bol. Mus. Nac. Hist. Nat. 29:230. 1970.

Eugenia colchaguensis R. A. Philippi, Linnaea 33:72. 1864.
Myrceugenia malvillana Kausel, Lilloa 17:51. 1949.

Shrub 2–4 m high; hairs golden brown to yellowish brown, more or less symmetrically dibrachiate, twisted; twigs densely lanate when young, glabrescent with age, strongly flattened at the nodes. Leaves opposite or verticillate, densely lanate below when young, less densely so to glabrous above when young, glabrescent on both surfaces with age, elliptic to obovate, 0.7–2(–3) cm long, 0.4–1.2(–1.5) cm wide, 1.4–2 times as long as wide; apex obtuse to rounded; base rounded to acute; petiole 1–2 mm long, ca. 1 mm thick, densely lanate when young, glabrescent with age, slightly channeled; midvein recessed proximally or not at all above, prominent proximally, indistinct distally below; lateral and marginal veins indistinct; blades light yellow green to grey green, lustrous or dull above, lighter beneath, coriaceous to subcoriaceous. Peduncles uniflorous, flattened, 0.8–1.7 cm long, ca. 1 mm wide, densely lanate, solitary or in pairs in the leaf axils; bracteoles lanceolate, 1.5–2.5 mm long, 0.7–1 mm wide, 2–2.8 times as long as wide, densely lanate within and without, subcoriaceous, clasping the hypanthium; calyx lobes ovate to broadly triangular, 2–3 mm long, 2–3.5 mm wide, 0.7–1.2(–1.4) times as long as wide, densely lanate distally to glabrous proximally within, densely lanate without, coriaceous, usually somewhat concave; hypanthium densely lanate, 1.2–2 mm long; disk 2–3 mm across, sparsely covered with hairs; style 5–9 mm long, sparsely pubescent to glabrous; stamens ca. 180–240, 5–8 mm long; anthers ca. 0.5 mm long when dry; petals concave, more or less orbicular, ca. 3–5 mm in diam.; ovary usually 3-locular; ovules 6–12 per locule; mature fruit yellow orange, ca. 7 mm in diam. (Fig. 12K).

DISTRIBUTION (Fig. 13B).—A large shrub known from very few collections made from Valparaíso to Malleco. Four new localities have come to my attention since the publication of my monograph of *Myrceugenia* (Landrum 1981), viz., Arauco: Paicaví, Jan 1929 (fl), *Claude-Joseph 5953* (US). Cautín: Nueva Imperial, Almago, 50 m, Dec 1943 (fl), *Montero 4794* (CONC). Curicó: Potrero Grande, 21 Jan 1927 (fl), *Barros 1899* (CONC). Valparaíso: Quilpué, Hacienda Las Palmas, Cerro Chivato, 1 Nov 1984 (fr), *Zollner* and *Ruiz 1* (ASU).

PHENOLOGY.—Flowering occurs in January and February. Fruits probably mature in spring months of October to December.

Myrceugenia colchaguensis can be distinguished from other species of Chilean Myrtaceae by a combination of: calyx lobes that are densely lanate without; yellowish, symmetrically dibrachiate, twisted hairs; small leaves; and uniflorous peduncles.

8.3. **Myrceugenia correifolia** (W. J. Hooker et Arnott) Berg, Linnaea 30:670. 1861.

Eugenia correaefolia W. J. Hooker et Arnott, Bot. misc. 3:319. 1833.
Eugenia maritima Barnéoud, *in* Gay, Fl. Chil. 2:391. 1847.
Luma correaefolia (J. W. Hooker et Arnott) Gray, U.S. Expl. Exped., Phan. 542. 1854.
Eugenia thalassaia Berg, Linnaea 27:179. 1856.
Myrceugenia johowi Gusinde, Anales Univ. Chile 104:307. 1917.
Myrceugenia thalassaia (Berg) Gusinde ex Fuentes, Bol. Mus. Nac. Hist. Nat. 13:108. 1930.
Myrceugenia maritima (Barnéoud) Kausel, Revisión de las Mirtáceas Chilenas 2. 1940.

Tree or shrub up to 4 m tall or perhaps taller; hairs reddish brown to whitish grey, appressed, dibrachiate, about symmetric; twigs densely pubescent when young, glabrescent with age. Leaves sparsely to densely pubescent below, glabrous to densely pubescent above, oval to elliptic, 2–7.5 cm long, 1–4.5 cm wide, 1.5–2.3 times as long as wide, the margins revolute, the whole leaf sometimes curling in dried specimens; apex broadly rounded or obtuse, less often acute; base rounded to broadly cuneate; petiole densely to sparsely pubescent, 2–5 mm long, 1–1.5 mm thick, scarcely channeled; midvein slightly recessed proximally to not at all distally, more pu-

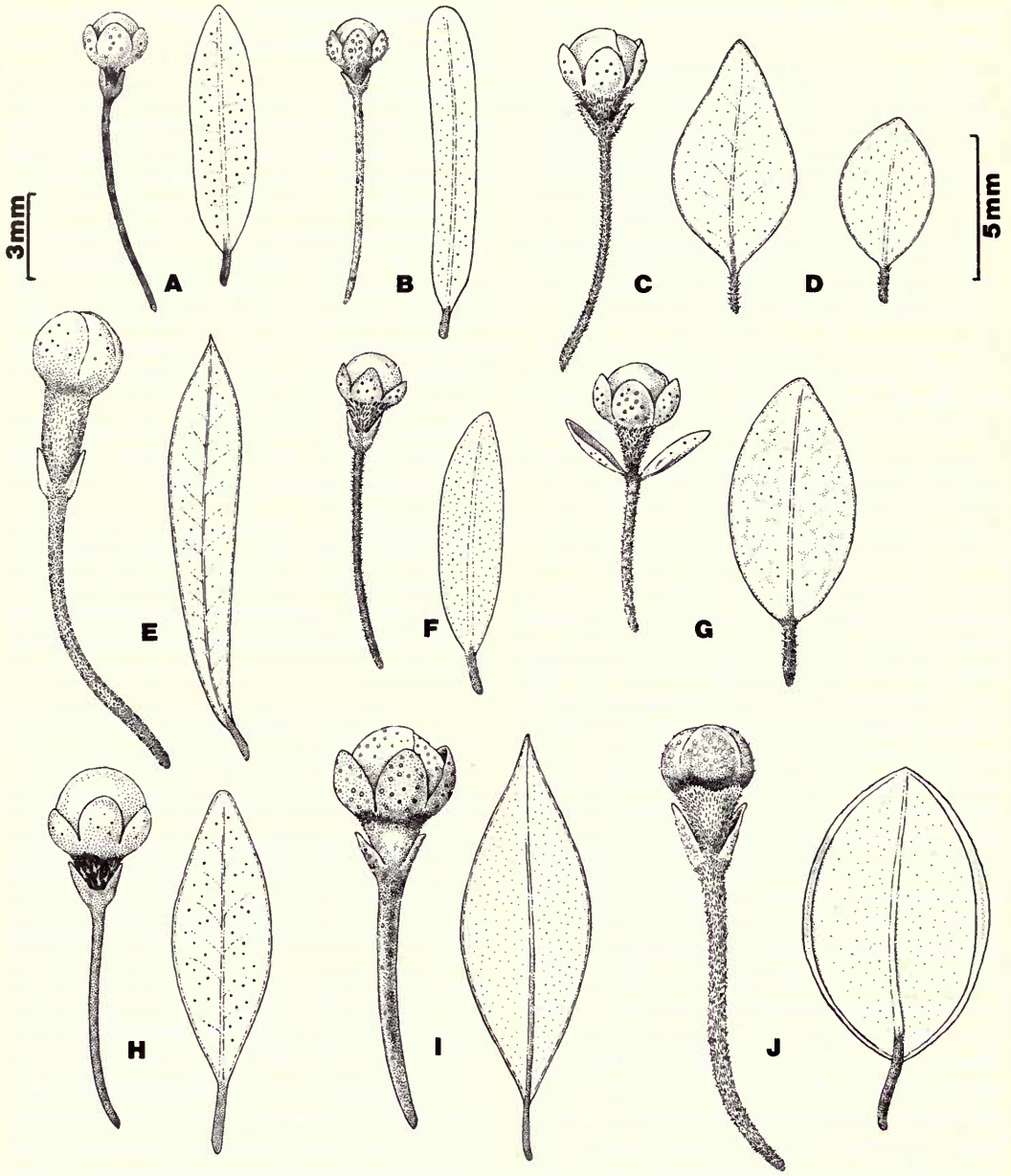
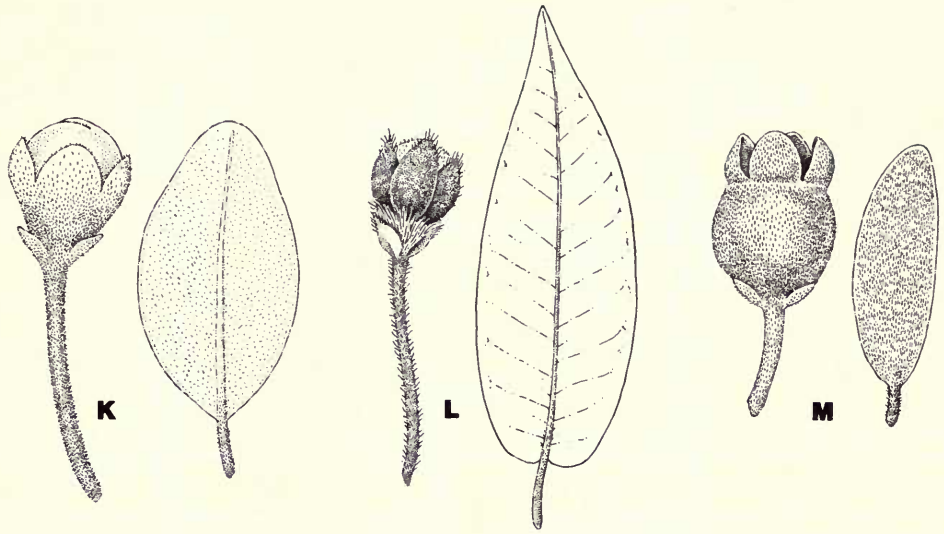


FIGURE 12. *Myrceugenia*. A, *M. parvifolia* (*Hollermayer 1200* at CAS). B, *M. leptospermoides* (*Aravena 18* at UC). C, *M. ovata* var. *ovata* (*West 4883* at UC). D, *M. ovata* var. *nannophylla* (*Landrum 3176* at MICH). E, *M. lanceolata* (*Reiche 17* at CAS). F, *M. pinifolia* (*Landrum 3090* at MICH). G, *M. obtusa* (*Morrison 16731* at UC). H, *M. chrysocarpa* (*Landrum 4376* at NY). I, *M. planipes* (bud from DS-30360, leaf from *Werdermann 1208* at CAS). J, *M. correifolia* (*Werdermann 900* at CAS). K, *M. colchaguensis* (*Claude Joseph 5953* at US). L, *M. fernandeziana* (*Pisano 1421* at UC). M, *M. rufa* (*Bertero 1170* at UC). Scale on left for flowers; scale on right for leaves. Relatively small leaves were used in this drawing for C, E, H, I, J, K and L. Drawn by Terry Bell.



bescent than surrounding blade above, prominent below; lateral veins indistinguishable or up to ca. 10 pairs barely visible; marginal veins equalling laterals; blades dull, light yellow green to light bluish green above, grey green to yellow green below, coriaceous. Peduncles uniflorous, flattened, 1–3.5 cm long, 1–1.5 mm wide, densely pubescent, solitary or in pairs in the leaf axils; bracteoles lanceolate, 3–7 mm long, 1–2 mm wide, 2.5–3.5 times as long as wide, coriaceous, glabrous to densely pubescent within, sparsely to densely pubescent without, clasping the hypanthium, becoming reflexed distally with age (rarely leaflike and not clasping the hypanthium); calyx lobes concave, coriaceous, very sparsely pubescent to glabrous within and without, conspicuously glandular, 2.5–4 mm long, 2.9–4.5 mm wide, 0.7–1 times as long as wide; hypanthium obconic, 2.5–4 mm long, densely pubescent; disk 3–4 mm across, sparsely pubescent; style 0.5–1 cm long, glabrous; stamens 130–200, 4–8 mm long; anthers 0.5–0.9 mm long when dry; petals suborbicular, concave, ca. 4–6 mm in diam., white to cream-colored; ovary 3–4-locular, the ovary wall thick, glandular; ovules 6–12 per locule. Fruit dark amber brown to black, glandular, 0.7–1 cm long, 0.4–0.8 cm wide, sparsely puberulent; seeds usually 3–4, 6–8 mm long, more or less oblong (Fig. 12J).

Distribution (Fig. 13C).—A shrub or small tree growing in coastal habitats from Coquimbo to Curicó.

Phenology.—Flowering from August to February. Fruits mature within a few months.

Myrceugenia correifolia is distinguished from other species of Chilean Myrtaceae by a combination of relatively large flowers, large leaves, and revolute leaf margins. It is occasionally confused with *M. exsucca* from which it differs in having a uniflorous inflorescence, bracteoles over 2 mm long, and strictly dibrachiate hairs.

8.4. **Myrceugenia exsucca** (A. P. de Candolle) Berg, Linnaea 30:671. 1861.

Eugenia exsucca A. P. de Candolle, Prodr. 3:278. 1828.
?*Eugenia temu* W. J. Hooker et Arnott, Bot. Beechey Voy. 56. 1832.
Eugenia multiflora W. J. Hooker et Arnott, Bot. misc. 3:322. 1833.
?*Luma temu* (W. J. Hooker et Arnott) Gray, U.S. Expl. Exped., Phan. 539. 1854.
Myrceugenia lechleriana Berg, Linnaea 27:133. 1856.
Myrceugenia camphorata Berg, Linnaea 27:134. 1856.
Eugenia exsucca [var.] *α peruviana* Berg, Linnaea 27:255. 1856.
Eugenia exsucca [var.] *β patagua* Berg, Linnaea 27:256. 1856.
?*Eugenia exsucca* [var.] *γ temu* (W. J. Hooker et Arnott) Berg, Linnaea 27:256. 1856.
?*Eugenia exsucca* [var.] *δ apiculata* Berg, Linnaea 27:257. 1856.
Eugenia pitra Berg, Linnaea 27:264. 1856.
Eugenia corralensis Philippi, Linnaea 33:72. 1864.
Myrceugenia multiflora (W. J. Hooker et Arnott) Kausel, Revisión de las Mirtáceas Chilenas 2. 1940; Revista Argent. Agron. 9:63. 1942.
Luma exsucca (A. P. de Candolle) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:525. 1941.

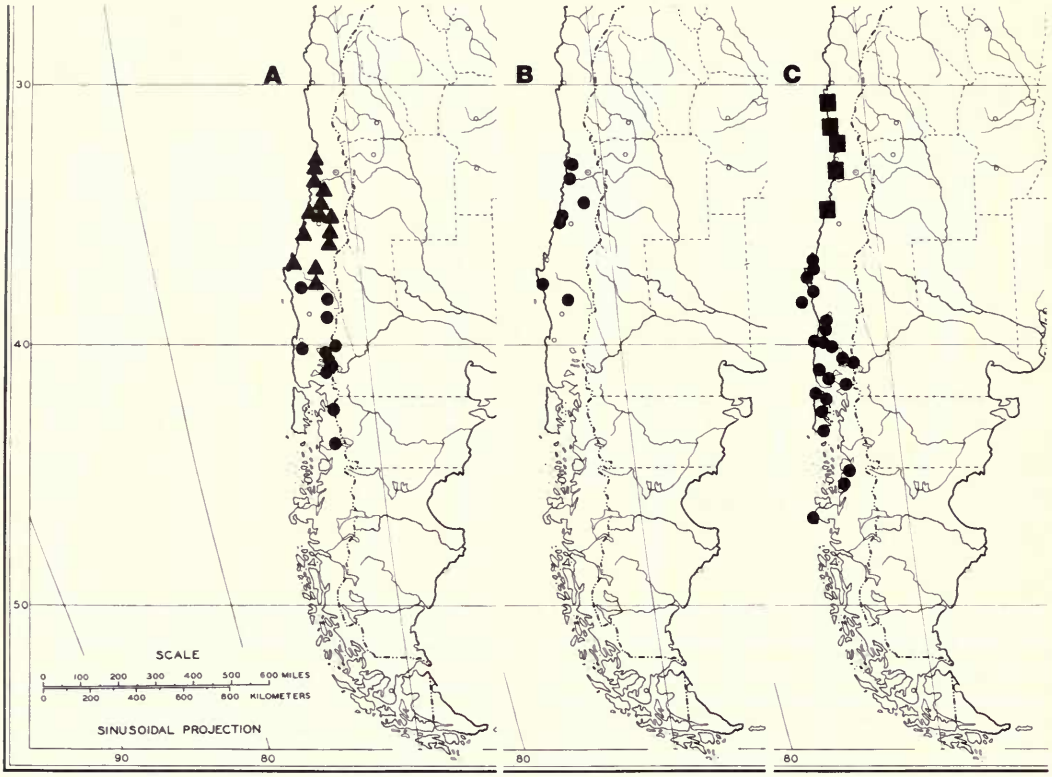


FIGURE 13. Distribution of *Myrceugenia chrysocarpa* (A, circles), *M. lanceolata* (A, triangles), *M. colchaguensis* (B, circles), *M. correifolia* (C, squares), and *M. planipes* (C, circles).

Luma pitra (Berg) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:525. 1941.

Luma corralensis (R. A. Philippi) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:525. 1941.

Tree up to ca. 12 m high, the bark light grey, rough with longitudinal fissures; hairs reddish brown to yellowish brown, simple or asymmetrically dibrachiate; twigs densely pubescent when young, the hairs more or less spreading, gradually deciduous or persisting until the young bark falls. Leaves suborbicular, elliptic, elliptic-obovate, or elliptic-ovate (1–)2–7.5(–12.5) cm long, (0.8–)1.5–3.5(–5) cm wide, 1.2–2.4 times as long as wide, sparsely puberulent to glabrous above, moderately to sparsely pubescent below when young, glabrescent with age; apex and base acute to rounded or less often acuminate; petiole unchanneled or weakly channeled, 1.5–6 mm long, 1–2 mm thick, sparsely to densely pubescent; midvein impressed for entire length or only proximally above, prominent below, often slightly excurrent; lateral veins indistinct or up to ca. 20 pairs visible; marginal veins equalling laterals in prominence or less prominent; blades coriaceous to subcoriaceous, dark or light grey green to reddish brown above, lightly yellow green to reddish tan below, usually strongly discolorous, the surfaces dull. Inflorescence a solitary flower, a dichasium, or less often a bracteate shoot, the multiflorous inflorescences 3–10 cm long, bearing up to ca. 10 flowers. Peduncles solitary or up to 3 in a row in the axils of leaves and bracts, flattened, 0.5–1 mm wide, densely pubescent; bracteoles lanceolate, 1–2 mm long, 0.3–0.5 mm wide, 2–5 times as long as wide, sparsely to densely pubescent within and without, subcoriaceous; calyx lobes ovate to ovate-oblong, concave, 1.6–2.8 mm long, 1.7–2.7 mm wide, 0.7–1.2 times as long as wide, subcoriaceous, sparsely to densely pubescent within and without, strongly reflexed after flowering; hypanthium obconic to subglobose, 2–4 mm long, densely pubescent; disk 2.5–3 mm across, densely to sparsely pubescent, slightly recessed in the center; stamens 170–275, 3–10 mm long; anthers 0.3–0.5 mm long; petals glabrous to sparsely pubescent, sub-

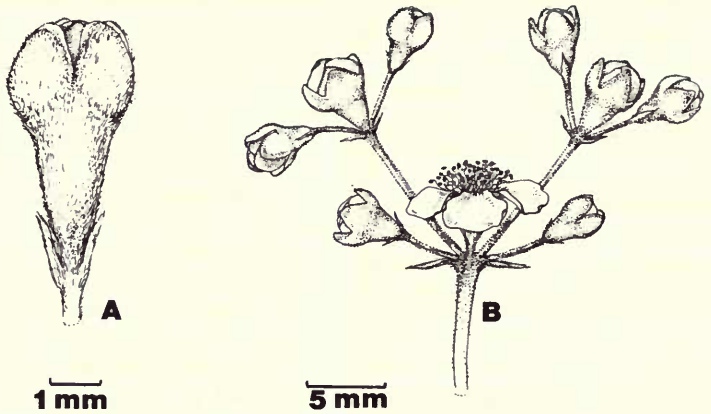


FIGURE 14. Flower and inflorescences of *Myrceugenia exsucca* (*Maldonado 21* at NY). A, flower showing two persistent bracteoles subtending the hypanthium. B, a dichasial inflorescence with superimposed branches. Drawn by Karen Douthit.

orbicular, 2–4 mm in diam., white to tan when dry; style 5–8 mm long, sparsely pubescent; ovary 2–4-locular; ovules 7–13 per locule. Fruit globose, about 6–8 mm in diam., yellow brown to orange brown when dry; seeds 2–9, subglobose to oblong, 3–5 mm long (Fig. 14).

DISTRIBUTION (Fig. 15B).—A common tree of relatively wet habitats (edges of lakes, marshes, along slow-moving rivers) from Coquimbo to Chiloé in Chile and from the Andes of Neuquén, Río Negro, and Chubut in Argentina.

PHENOLOGY.—Flowering from January to March. Fruits seem to mature from September to November.

Myrceugenia exsucca is distinguished by its dichasial inflorescences, persistent bracteoles, and broad, usually subelliptic leaves. It hybridizes with *M. lanceolata* and *M. ovata* var. *nannophylla* (Landrum 1975, 1981). It is occasionally confused with *B. cruckshanksii,* which has a similar inflorescence structure, leaf size and shape, and habitat preference. *Myrceugenia exsucca* can be distinguished from that species by its persistent bracteoles, leaf apexes that are not emarginate, and rough-fissured bark.

8.5. **Myrceugenia fernandeziana** (W. J. Hooker et Arnott) Johow, Estud. Fl. Juan Fernández 94. 1896.

Myrtus fernandeziana W. J. Hooker et Arnott, Bot. misc. 3: 316. 1833.

Eugenia lumilla R. A. Philippi, Bot. Zeitung (Berlin) 14:643. 1856.

Eugenia fernandeziana (W. J. Hooker et Arnott) Barnéoud *in* Gay, Fl. Chil. 2:392. 1847.

Myrceugenia luma Berg, Linnaea 30:671. 1860.

Luma fernandeziana (W. J. Hooker et Arnott) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:526. 1941.

Nothomyrcia fernandeziana (W. J. Hooker et Arnott) Kausel, Lilloa 13:148. 1948 ("1947").

Tree up to 25 m high, the bark smooth, mottled; hairs simple, usually spreading, whitish; twigs moderately to sparsely pubescent when young, glabrescent with age. Leaves very sparsely pubescent to glabrous, ovate to lanceolate, 2.8–7.3 cm long, 1.2–2.3 cm wide, 2–4 times as long as wide; apex acute to acuminate, the tip usually blunt; base slightly cordate to narrowly rounded; petiole 2–5 mm long, moderately pubescent to glabrous when young, losing any pubescence with age, often rough with cracks and wrinkles, barely channeled, reddish brown to blackish; midvein about flush with blade to slightly raised, prominent, with longitudinal wrinkles above and below; lateral veins prominent, up to about 40 pairs visible, the reticulate secondary veins numerous; marginal veins equalling laterals in prominence, arching slightly between them; blades light yellow green to darker grey green above (rarely drying reddish brown), the same color or slightly lighter below, coriaceous; flowers mainly aggregated together in bracteate shoots of 4–12, the shoots 1–3 cm long, either solitary or seriate at the nodes, terminating in a vegetative bud or flower. Peduncles solitary or in pairs in the axils of bracts (perhaps also occasionally in the axils of leaves), 2–11 mm long, ca. 0.5 mm wide, densely to sparsely pubescent; bracts and bracteoles ovate, 1–2.5 mm long, ca. 1 mm wide, membranous, caducous at anthesis or before, sparsely pubes-

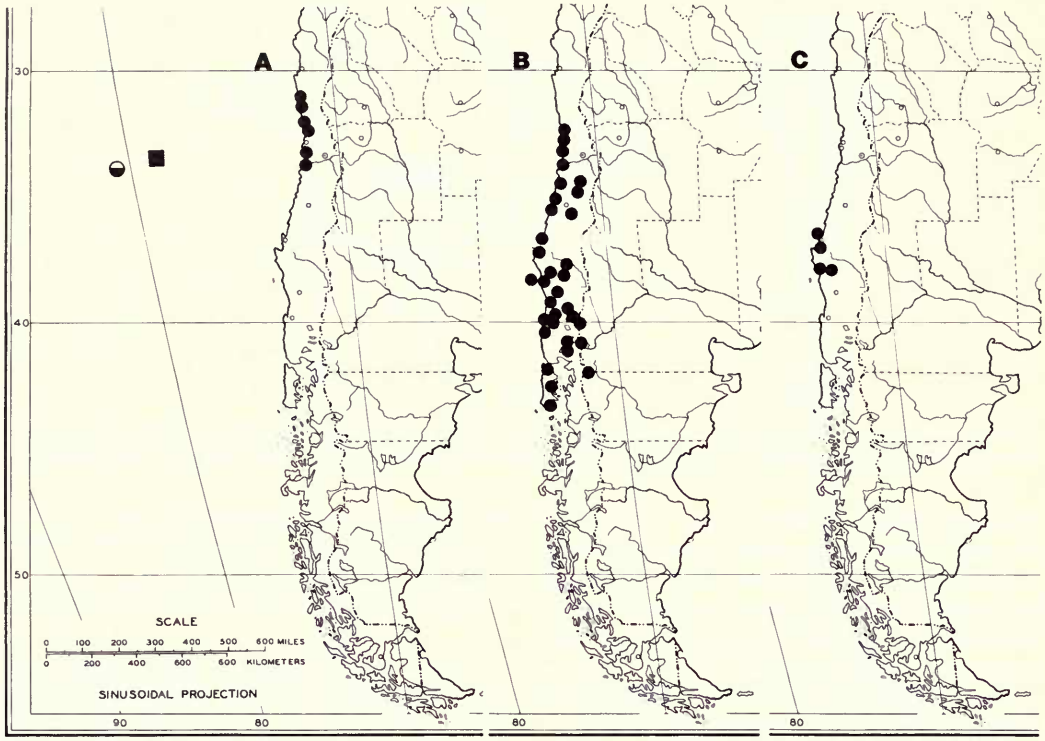


FIGURE 15. Distribution of *Myrceugenia fernandeziana* (A, square), *M. schulzei* (A, half circle), *M. rufa* (A, whole circle), *M. exsucca* (B, circle), and *M. leptospermoides* (C, circle).

cent to glabrous within and without, some bracts serving as bud scales; calyx lobes ovate, strongly concave, more or less acute, 1.6–4 mm long, 1.6–3.5 mm wide, 1–1.4 times as long as wide, membranous to slightly fleshy, sparsely pubescent without, sparsely to densely pubescent within; hypanthium obconic, densely pubescent, 1.5–3 mm long; disk 2–3 mm across, moderately to densely pubescent, sometimes becoming slightly convex during maturation; style densely to sparsely pubescent, 6–9 mm long; stamens 40–80, 5–10 mm long; anthers 0.5–0.8 mm long when dry; petals more or less orbicular to slightly elongate, 2–4 mm in diam.; ovary 2–3-locular; ovules (1–)3–7 per locule. Fruit orange when fresh, darkening when dry, few seeded (Fig. 12L).

DISTRIBUTION (Fig. 15A).—Known only from Masatierra, of the Juan Fernández Islands, where it is perhaps the most common tree.

PHENOLOGY.—Flowering from August to December. Fruits probably mature in July and August.

LOCAL NAME AND USE.—Luma. The wood has been used as a building material in the past.

Myrceugenia fernandeziana is distinguished by its large, usually lanceolate leaves with the midveins not impressed and somewhat wrinkled.

8.6. **Myrceugenia lanceolata** (Jussieu ex Jaume Saint-Hilaire) Kausel, Lilloa 13:135. 1948 ("1947").

Myrtus lanceolata Jussieu ex Jaume Saint-Hilaire, *in* Duhamel, Traité arbr. arbust., ed. 2, 1:208. 1800–1803.

Eugenia dombeyana A. P. de Candolle, Prodr. 3:276. 1828.

Myrtus gudilla Colla, Mem. Reale Accad. Sci. Torino 37:66. (preprints May 1833) late 1834.

Eugenia stenophylla W. J. Hooker et Arnott, Bot. misc. 3:322. 1833.

Eugenia gudilla (Colla) Barnéoud, *in* Gay, Fl. Chil. 2:396. 1847.

Luma stenophylla (W. J. Hooker et Arnott) Gray, U.S. Expl. Exped., Phan. 540. 1854.

Eugenia stenophylla [var.] *α angustifolia* Hooker ex Berg, Linnaea 27:254. 1856.

Eugenia stenophylla [var.] *β latifolia* Hooker ex Berg, Linnaea 27:254. 1856.

Myrceugenia stenophylla (W. J. Hooker et Arnott) Berg, Linnaea 30:670. 1861.

Luma dombeyana (A. P. de Candolle) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:525. 1941.

Shrub up to 3 m high; hairs reddish brown to whitish, a mixture of simple and dibrachiate; twigs reddish when young, later brown or grey, densely to sparsely pubescent when young, soon glabrescent, the hairs spreading, mainly simple and asymmetrically dibrachiate. Leaves oblanceolate to linear, (1.5–)2–5 cm long, 0.2–1.5(–2) cm wide, (2.5–)3–15 times as long as wide, glabrous or with a few scattered appressed dibrachiate hairs below; apex acute, acuminate, obtuse, or rarely rounded; base acute or cuneate, normally tapering from above the middle of the leaf; petiole unchanneled or weakly channeled, sparsely pubescent to glabrous, 1–4(–5) mm long, 0.5–1 mm thick; midvein shallowly impressed for nearly entire length above, moderately prominent below; lateral veins indistinct or up to ca. 10 pairs of sharply ascending veins faintly visible; marginal veins equalling or less prominent than the laterals; blades coriaceous, dark grey green to reddish brown above, lighter grey green, yellow green or tan below when dry, normally strongly discolorous, the surfaces dull. Peduncles uniflorous or bearing a 3 (rarely more)-flowered dichasium, flattened, 0.4–3.5 cm long, 0.5–1 mm wide, densely to sparsely pubescent, solitary or in pairs (rarely triplets) in the leaf axils, the terminal flower of the dichasium usually without a stalk beyond the bracteoles; bracteoles of solitary flowers and lateral flowers lanceolate, 1.5–3 mm long, 0.5–1 mm wide, 2.5–4 times as long as wide, subcoriaceous, sparsely to densely pubescent without, sparsely pubescent to glabrous within, clasping the hypanthium, the bracteoles of the central flowers of the dichasium similar but larger, up to 15 mm long; calyx lobes ovate to oblong, 1.8–4 mm long, 1.5–3 mm wide, 1–1.7 times as long as wide, submembranous, sparsely pubescent distally to glabrous within, sparsely to moderately pubescent without, concave, becoming strongly reflexed after flowering; petals glabrous to sparsely pubescent, suborbicular, 2–4 mm in diam., white to tan when dry; hypanthium more or less obconic, contracted below the calyx lobes, 2–5 mm long, densely pubescent; disk sparsely to densely pubescent, 2–3 mm across, recessed in the center; stamens 100–200, 3–7 mm long; anthers 0.3–0.5 mm long when dry; style 6–10 mm long, sparsely pubescent; ovary 2–3-locular; ovules 4–8 per locule. Fruit globose to pyriform, 7–10 mm long, yellow, slightly spongy, the walls thin, not noticeably glandular; seeds 2–8 in fruits seen, oblong, 3–5 mm long (Fig. 12E).

Distribution (Fig. 13A).—A shrub growing along streams and rivers from Valparaíso to Malleco.

Phenology.—Flowering mainly in March and February; fruits probably mature mostly in September and October.

Myrceugenia lanceolata can be distinguished by its oblanceolate, strongly discolorous leaves, and dichasial inflorescence.

8.7. **Myrceugenia leptospermoides** (A. P. de Candolle) Kausel, Revisión de las Mirtáceas Chilenas 2. 1940; Revista Argent. Agron. 9: 52. 1942.

Eugenia leptospermoides A. P. de Candolle, Prodr. 3:266. 1828.
Eugenia leptospermoides [var.] α *microphylla* Berg, Linnaea 27:143. 1856.
?*Eugenia leptospermoides* [var.] β *latifolia* Berg, Linnaea 27: 143. 1856.
Eugenia leptospermoides [var.] γ *longifolia* Berg, Linnaea 27: 143. 1856.
Eugenia thymifolia R. A. Philippi ex Reiche, Anales Univ. Chile 98:719. 1897; Fl. Chile 2:303. 1898.

Shrub 0.5–2 m high; hairs reddish brown, a mixture of simple and dibrachiate; twigs grey to whitish grey, densely pubescent when young, the hairs persisting until the first bark falls. Leaves oblong to linear, 4–15 mm long, 1.5–3 mm wide, 2.7–7 times as long as wide, glabrous or with a few scattered hairs beneath; apex obtuse; base obtuse to acute; midvein slightly impressed or not at all above, moderately prominent below; lateral and marginal veins indistinct; blades subcoriaceous, dull grey green or brownish green above, lighter, often yellow green below. Peduncles uniflorous, slightly flattened, 2–8 mm long, 0.2–0.3 mm wide, densely pubescent, solitary (rarely in pairs) in the axils of leaves; bracteoles ovate to oblong-lanceolate, blunt, 0.4–1.5 mm long, 0.3–0.7 mm wide, 1.3–2.3 times as long as wide, sparsely pubescent to glabrous within and without, subcoriaceous, loosely clasping the hypanthium; calyx lobes ovate, oblong-ovate to suborbicular, 1–2 mm long, 1–1.5 mm wide, 0.8–1.4 times as long as wide, glabrous to very sparsely pubescent within and without, membranous to subcoriaceous, concave, usually tinged with

red; hypanthium densely pubescent; stamens 60–90, ca. 3–5 mm long; anthers 0.2–0.4 mm long when dry; petals suborbicular, 1.5–2.5 mm in diam.; style ca. 4–5 mm long, glabrous to very sparsely pubescent; ovary 2–3-locular; ovules 2–6 per locule. Fruit reddish purple, globose, 4–5 mm in diam.; seeds 1–2 in fruits seen, oblong, 2–3 mm long (Fig. 12B).

Distribution (Fig. 15C).—A shrub of Concepción, Arauco, and Malleco apparently confined to humid or foggy habitats.

Phenology.—Flowering in February and March; fruits seem to mature about 1 yr later.

Myrceugenia leptospermoides can be distinguished by its linear to oblong leaves 1.5–3 mm wide and pubescent peduncles.

8.8 **Myrceugenia obtusa** (A. P. de Candolle) Berg, Linnaea 30:699. 1861.

Eugenia obtusa A. P. de Candolle, Prodr. 3:266. 1828.
Myrtus raran Colla, Mem. Reale Accad. Sci. Torino 37:66. (preprints May 1833) late 1834.
Eugenia raran (Colla) Barnéoud, *in* Gay, Fl. Chil. 2:388. 1847.
Luma obtusa (A. P. de Candolle) A. Gray, U.S. Expl. Exped., Phan. 541. 1854.
Myrceugenia chilensis Berg, Linnaea 27:132. 1956.
Eugenia polyantha Philippi, Linnaea 28:639. 1857.
Myrceugenia obtusa [var.] α *raran* (Colla) Berg, Linnaea 30: 699. 1861.
Myrceugenia obtusa [var.] β *berteroana* Berg, Linnaea 30:699. 1861.
Myrceugenia obtusa [var.] γ *polyantha* (Philippi) Berg, Linnaea 30:699. 1861.

Shrub or small tree 2–8 m high; hairs reddish brown, a mixture of simple and dibrachiate; twigs reddish brown when young, becoming greyish brown with age, densely pubescent when young, the hairs spreading, persisting until the first bark exfoliates. Leaves opposite to subopposite, glabrous or with a few scattered hairs, elliptic to ovate, 1–3 cm long, 0.6–2(–2.5) cm wide, 1–2.2 times as long as wide; apex bluntly acute, obtuse or rounded; base acute, obtuse to rounded (rarely slightly cordate); midvein not noticeably impressed above, moderately prominent to indistinct below; lateral veins indistinct or up to ca. 5 pairs faintly visible; marginal veins indistinct; blades coriaceous, often brittle even when alive, grey green to brown above, lighter grey green or brown below, the surfaces dull or lustrous, often wrinkled, with the appearance of shiny paper. Peduncles uniflorous, flattened, 2–15 mm long, 0.4–0.6 mm wide, moderately to densely pubescent, solitary in the axils of leaves; bracteoles leaflike, petiolate, linear, oblong, elliptic or spatulate, 2–6 mm long, 0.5–2.5 mm wide, 2–4.5 times as long as wide, subcoriaceous, glabrous to sparsely pubescent, not clasping the hypanthium; calyx lobes ovate to oblong, 2–4 mm long, 1.7–2.5 mm wide, 1–1.8 times as long as wide, submembranous, glabrous within, sparsely pubescent to glabrous without, concave; petals suborbicular, 3–4 mm long; hypanthium densely pubescent, 1–2 mm long, more or less obconic; disk 2–2.5 mm across, sparsely pubescent to glabrous; stamens 90–190, 4–8 mm long; anthers 0.2–0.4 mm long when dry; style 5–7 mm long, glabrous to sparsely pubescent; ovary 2–4-locular; ovules 5–9(–12) per locule. Fruit dark purple black, globose to elongate, 5–10 mm in diam.; seeds 3–4 in fruits seen, 4–5 mm in diam. (Fig. 12G).

Distribution (Fig. 16A).—A shrub or small tree of coastal Coquimbo to the central valley of Cautín.

Phenology.—Flowering in December and January; fruits maturing from April to November.

Myrceugenia obtusa is easily distinguished by small obtuse, mainly elliptic leaves and leafy bracteoles.

8.9. **Myrceugenia ovata** (W. J. Hooker et Arnott) Berg, Linnaea 30:670. 1861.

Eugenia ovata W. J. Hooker et Arnott, Bot. misc. 3:319. 1833.

Shrub or small tree up to ca. 8 m high, with moderately rough, scaly bark when large; hairs whitish to reddish brown, a mixture of simple and dibrachiate; twigs densely pubescent when young, glabrescent with age, the young bark smooth, grey or light brown. Leaves glabrous to sparsely pubescent beneath, entirely glabrous to puberulent along the midvein above, ovate to elliptic, 0.3–4 cm long, 0.2–2 cm wide, 1.2–2.6 times as long as wide; apex acute, acuminate, obtuse, or rounded; base acute to truncate; petiole channeled, densely to sparsely pubescent, 1–5 mm long, 0.5–1 mm thick; midvein impressed for entire length or only proximally above, moderately prominent below; lateral veins indistinguishable or up to ca. 10 pairs faintly visible; marginal veins equalling laterals in prominence; blades grey green, reddish brown, or yellow green above, lighter below, coriaceous to submem-

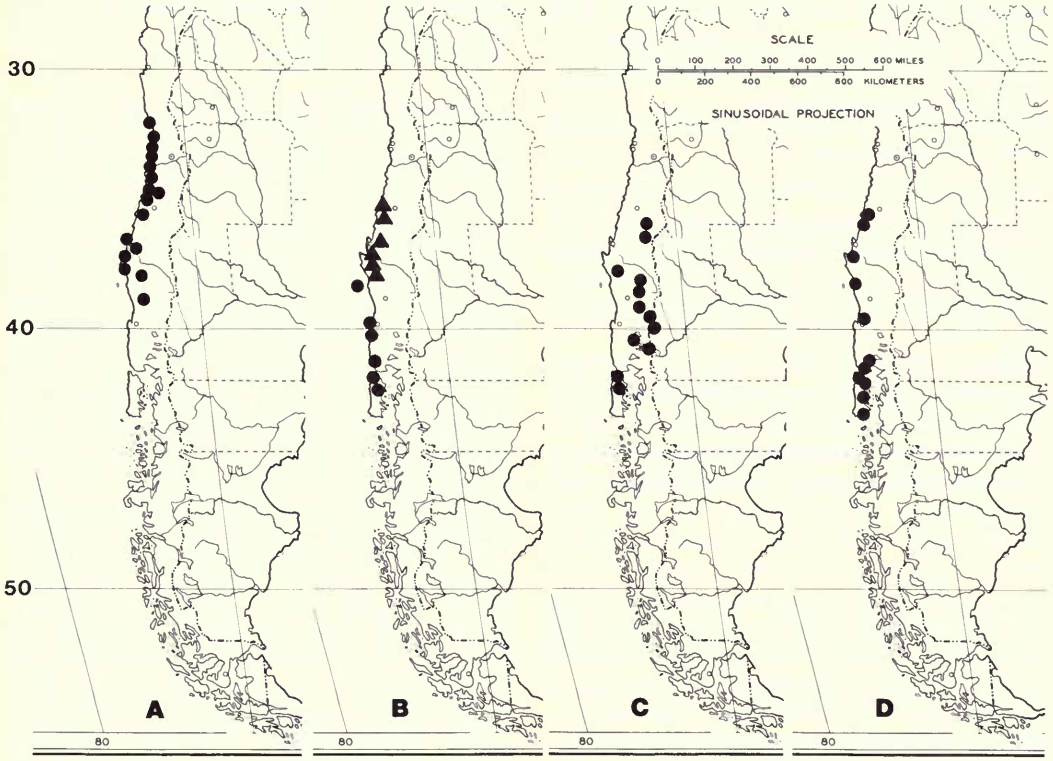


FIGURE 16. Distribution of *Myrceugenia obtusa* (A, circles), *M. ovata* var. *ovata* (B, circles), *M. pinifolia* (B, triangles), *M. ovata* var. *nannophylla* (C, circles), and *M. parvifolia* (D, circles).

branous, the upper surface dull or lustrous. Peduncles uniflorous, flattened, 0.2–1.5 cm long, 0.3–0.5 mm wide, densely pubescent, solitary in the axils of leaves; bracteoles ovate to lanceolate, 0.5–1.8 mm long, 0.3–1 mm wide, 1.2–3.8 times as long as wide, sparsely pubescent to glabrous within and without, subcoriaceous to membranous, clasping the hypanthium; calyx lobes triangular to ovate, 1–2.5(–3) mm long and wide, 0.8–1.4 times as long as wide, sparsely pubescent to glabrous within and without, subcoriaceous to membranous, concave; hypanthium densely pubescent, obconic, 1–2 mm long; disk ca. 1–2.5 mm across, sparsely pubescent to glabrous; stamens 50–130, 3–8 mm long; anthers 0.2–0.4 mm long; petals glabrous, suborbicular, 1.5–4 mm in diam.; ovary 2–4-locular; ovules 3–11 per locule. Fruit globose, ca. 4–7 mm in diam., yellowish to orange, few seeded, the seeds ca. 3–5 mm long.

There are four varieties of *Myrceugenia ovata*: two of southeastern Brazil and two of temperate western South America (Landrum 1981).

Myrceugenia ovata of western South America is distinguished by ovate leaves, and persistent, small, ovate to lanceolate clasping bracteoles. Var. *ovata* has occasionally been confused with *Luma apiculata* and *Amomyrtus luma*. Both have deciduous bracteoles. *Amomyrtus* has pentamerous flowers, whereas in *Myrceugenia* they are tetramerous.

KEY TO VARIETIES OF *MYRCEUGENIA OVATA* IN CHILE

1. Leaves ovate, mainly 1–2 cm long, often surpassing 2 cm, the apex acute to acuminate; along the coast and in the coastal mountains of Chile ..... var. *ovata*
1. Leaves ovate to elliptic, mainly under 1 cm long, rarely surpassing 1.5 cm long, the apex obtuse to rounded; mainly Andean ..... var. *nannophylla*

8.9a. **Myrceugenia ovata** var. **ovata**

Eugenia ovata W. J. Hooker et Arnott, Bot. misc. 3:319, as to type, 1833.

Eugenia cumingii W. J. Hooker et Arnott, Bot. misc. 3:319. 1833.
Eugenia trichocarpa Philippi, Linnaea 28:688. 1858.
Luma ovata (W. J. Hooker et Arnott) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:524. 1941.
Luma cumingii (W. J. Hooker et Arnott) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:524. 1941.

Leaves mainly ovate, 0.6–4 cm long, 0.5–2 cm wide, ca. 1.2–2.2 times as long as wide; apex acute to acuminate. Peduncles ca. 3–15 mm long; calyx lobes 1.1–2.5(–3) mm long, 1.4–2.5(–3) mm wide; hypanthium 1–2 mm long; stamens 50–130; ovules 5–11 per locule (Fig. 12C).

DISTRIBUTION (Fig. 16B).—An understory tree in coastal forests from Arauco (Isla Mocha), and from Valdivia to Chiloé.

PHENOLOGY.—Flowering from December to February; fruiting period probably during the winter months.

8.9b. **Myrceugenia ovata** var. **nannophylla** (Burret) Landrum, Brittonia 32(3):374. 1980.

Luma nannophylla Burret, Repert. Spec. Nov. Regni Veg. 50: 50. 1941.
Myrceugenia montana Kausel, Revista Argent. Agron. 9:55. 1942.
Myrceugenia valientei Kausel, Revista Argent. Agron. 11:323. 1944.
Myrceugenia nannophylla (Burret) Kausel, Revista Argent. Agron. 18:233. 1951.

Leaves mainly ovate, elliptic toward the northern end of range, 3–16 mm long, 2–8 mm wide, 1.2–2.6 times as long as wide; apex obtuse to rounded. Peduncles ca. 2–15 mm long; calyx lobes 1–2.2 mm long, 1–2 mm wide; hypanthium 1–2 mm long; stamens 50–110; ovules 3–8 per locule (Fig. 12D).

DISTRIBUTION (Fig. 16C).—A shrub, often growing near lakes, from the Andes of Linares to Chiloé in Chile and in the vicinity of Lago Nahuel Huapi in Neuquén, Argentina. Sometimes associated with *Nothofagus antarctica* in what appear to be cold air pockets.

PHENOLOGY.—Flowering from February to April; fruits seem to mature about 12 mo later.

8.10. **Myrceugenia parvifolia** (A. P. de Candolle) Kausel, Revisión de las Mirtáceas Chilenas 2. 1940; Revista Argent. Agron. 9: 53. 1942.

Eugenia parvifolia A. P. de Candolle, Prodr. 3:266. 1828.
Luma baeckeoides Grisebach, Syst. Bemerk. 32. 1854; Abh. Königl. Ges. Wiss. Göttingen 6:120. 1856.

Shrub or small tree 1–5 m high; hairs whitish to reddish brown, a mixture of simple and dibrachiate; twigs light grey to reddish brown, densely pubescent when young, the hairs spreading, deciduous with the young twig bark. Leaves glabrous or with scattered symmetric dibrachiate hairs, narrowly elliptic, oblong or lanceolate, 1–2.6 cm long, 0.3–0.7 cm wide, (2.2–)2.7–4.8 times as long as wide; apex and base acute to obtuse; midvein impressed for entire length to not at all above, moderately prominent to indistinct below; lateral veins indistinct or up to 5 pairs faintly visible; marginal veins equalling laterals in prominence; blades subcoriaceous to submembranous, dull grey green, often tinged with reddish brown above, lighter grey green or yellow green below. Peduncles uniflorous, slightly flattened, 5–14 mm long, 0.3–0.4 mm wide, glabrous or with a few scattered hairs, solitary in the axils of leaves; bracteoles ovate to lanceolate, 0.5–1 mm long, 0.2–0.5 mm wide, 1.3–3.5 times as long as wide, subcoriaceous, sparsely pubescent to glabrous within and without, loosely clasping the hypanthium; calyx lobes ovate to oblong, 1.2–2.3 mm long, 1–2 mm wide, 1–1.7 times as long as wide, glabrous or with a few scattered hairs within and without, submembranous, concave; hypanthium obconic, 0.8–1.5 mm long, sparsely pubescent, the hairs whitish, appressed; disk 1–2 mm across, very sparsely pubescent to glabrous; stamens 60–100; anthers 0.2–0.3 mm long; ovary 2–3-locular; ovules 3–8 per locule. Fruit globose, ca. 7 mm in diam.; seeds few, oblong, 3–4 mm long (Fig. 12A).

DISTRIBUTION (Fig. 16D).—An understory shrub or tree from Arauco to Chiloé.

PHENOLOGY.—Flowering mainly in February and March; fruits probably maturing in October and November.

Myrceugenia parvifolia is distinguished by its relatively narrow, small leaves, and glabrous peduncles.

8.11. **Myrceugenia pinifolia** (F. Philippi) Kausel, Revisión de las Mirtáceas Chilenas 2. 1940; Revista Argent. Agron. 9:54. 1942.

Eugenia pinifolia F. Philippi, Annales Univ. Chile 84:758. 1893.
Myrceugenia stenophylla var. *pinifolia* (F. Philippi) Reiche, Anales Univ. Chile 98:713. 1897; Fl. Chile 2:297. 1898.

Shrub up to ca. 2 m high; hairs reddish brown to whitish, a mixture of simple and dibrachiate; twigs densely pubescent when young, glabrescent with age, the hairs usually spreading. Leaves narrowly elliptic to linear, 1–3 cm long, 0.2–0.8 cm wide, 3–12 times as long as wide, glabrous to very sparsely pubescent, the hairs appressed, dibrachiate; apex and base acute or obtuse; petiole channeled, densely pubescent, 0.5–3 mm long, 0.3–0.8 mm thick; midvein slightly impressed proximally to not at all above, moderately prominent to indistinct below; lateral and marginal veins indistinct; blades coriaceous to subcoriaceous, grey green, often dark above, light grey green to light yellow green below, usually strongly discolorous, the surfaces dull. Peduncles uniflorous, 5–10 mm long, 0.3–0.5 mm wide, densely pubescent, solitary in the axils of leaves; bracteoles ovate to lanceolate, (0.5–)0.7–1.8 mm long, 0.3–1 mm wide, 1.3–2.6 times as long as wide, subcoriaceous, glabrous or nearly so within, sparsely pubescent without, clasping the hypanthium; calyx lobes bluntly ovate to shortly oblong, 1–2.3 mm long, 1–2.5 mm wide, 0.8–1.3 times as long as wide, subcoriaceous, glabrous or nearly so within, sparsely pubescent without, concave; hypanthium obconic, 1.5–2.5 mm long, densely pubescent; disk sparsely pubescent to glabrous, 1.5–2.5 mm across; style glabrous, 6–7 mm long; stamens 100–140, 3–8 mm long; anthers 0.3–0.4 mm long when dry; petals glabrous, suborbicular, ca. 3 mm in diam.; ovary 2-locular; ovules 6–12 per locule. Fruit unknown (Fig. 12F).

Distribution (Fig. 16B).—A shrub growing along streams and around lakes from the coastal cordillera westward, from Maule to Arauco.

Phenology.—Flowering in January and February; fruiting period probably during the winter months.

Myrceugenia pinifolia is distinguished by its small, narrow, discolorous leaves, and uniflorous, pubescent peduncles. It is very similar to *M. ovata* var. *nannophylla*. The most notable difference is in leaf shape (see Fig. 12D and F). *Myrceugenia pinifolia* is a coastal species, usually found below 200 m, whereas *M. ovata* var. ovata is a mainly Andean species growing above 500 m.

8.12. **Myrceugenia planipes** (W. J. Hooker et Arnott) Berg, Bot. Zeitung (Berlin) 16:250. 1858; Linnaea 30:670. 1861.

Eugenia planipes W. J. Hooker et Arnott, Bot. misc. 3:323. 1833.
Eugenia planipes [var.] *α genuina* Berg, Linnaea 27:162. 1856.
Eugenia planipes [var.] *β grandiflora* Berg, Linnaea 27:162. 1856.
Eugenia distoma Berg, Linnaea 27:155. 1856.
Myrcia planipes (W. J. Hooker et Arnott) Kiaerskou, Enum. Myrt. bras. 115. 1893.
Myrceugenia distoma (Berg) Kausel, Revista Argent. Agron. 9:238. 1942.

Small tree up to ca. 8 m high; hairs whitish, yellowish, or less often reddish brown, symmetrically dibrachiate, appressed; twigs sparsely to densely pubescent when young, glabrescent with age, the bark grey, often persisting as strips beneath the leaf bases. Leaves moderately to sparsely pubescent below when young, glabrescent with age, elliptic, 2.2–8 cm long, 1–3 cm wide, 2–3.4 times as long as wide; apex acuminate, less often acute; base cuneate to acuminate; petiole channeled, 2–6 mm long, 1–2 mm thick, densely to sparsely pubescent, becoming less so with age; midvein impressed for entire length or nearly so above, prominent below; lateral veins indistinguishable or up to ca. 30 pairs faintly visible; marginal veins equalling laterals in prominence; blades drying light to dark grey green or reddish brown above, lighter yellow green, grey green, or tan beneath, coriaceous. Peduncles strongly flattened, 0.7–3 cm long, ca. 1 mm wide, sparsely to moderately pubescent, solitary or up to 3(–4) in the axils of leaves or, less often, of bracts; bracteoles ovate to lanceolate, 1.9–3.1 mm long, 0.8–1.3(–1.7) mm wide, 1.4–3 times as long as wide, sparsely pubescent within and without, clasping the hypanthium or somewhat reflexed; calyx lobes broadly ovate, concave, 1.8–3 mm long, 2.5–4 mm wide, 0.5–0.8(–1.2) times as long as wide, coriaceous, sparsely pubescent to glabrous within and without; hypanthium hemispherical, densely pubescent, 1.5–4 mm long, usually prolonged 1–1.5 mm past the ovary; disk 2.5–4 mm across, sparsely pubescent to glabrous; style ca. 1 cm long, glabrous; stamens 120–220, 7–12 mm long; anthers 0.4–0.8 mm long when dry; petals suborbicular, 3–6 mm in diam.; ovary 3–4-locular; ovules 4–11(–13) per locule. Fruit globose, 0.8–1 cm in diam., purplish black; seeds few, ca. 6 mm in diam. (Fig. 12I).

Distribution (Fig. 13C).—An understory tree,

usually growing below 700 m, from Arauco to Aisén in Chile and on the Quetrihué peninsula in Lago Nahuelhuapi, Neuquén, Argentina.

PHENOLOGY.—Flowering mainly in January and February; fruits maturing in November and December.

Myrceugenia planipes is distinguished by relatively large, elliptic leaves that are usually acuminate at base and apex. It is most frequently confused with *M. chrysocarpa.* They are compared directly in lead 17 of the key.

8.13. **Myrceugenia rufa** (Colla) Skottsberg ex Kausel, Lilloa 13:134. 1948 ("1947").

Myrtus rufa Colla, Mem. Reale Accad. Sci. Torino 37:66. (preprints May 1833) late 1834.
Eugenia ferruginea W. J. Hooker et Arnott, Bot. misc. 3:319. 1 Aug 1833.
Eugenia rufa (Colla) Barnéoud *in* Gay, Fl. Chil. 2:388. 1847.
Luma ferruginea (W. J. Hooker et Arnott) A. Gray, U.S. Expl. Exped., Phan. 15:542. 1854.
Myrceugenia ferruginea (W. J. Hooker et Arnott) Reiche, Anales Univ. Chile 98:710. 1897; Fl. Chile 2:294. 1898.
Luma rufa (Colla) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:524. 1941.

Shrub 1–2 m high; hairs reddish brown to whitish, symmetrically dibrachiate, appressed; twigs densely pubescent when young, the hairs persisting until the first bark falls, the original bark splitting in a reticulate fashion, whitish grey, the new inner bark at first reddish brown, becoming whitish grey. Leaves densely strigose-pubescent beneath, puberulent above, sometime glabrescent with age, broadly to narrowly elliptic, ovate or oblong, 0.5–1.8 cm long, 0.2–0.5 cm wide, 1.2–4.5 times as long as wide, the margin revolute; petiole densely pubescent, sometimes glabrescent with age, 1–2 mm long, not noticeably channeled; veins all indistinct above and below, or the midvein faintly visible; blades light bluish green to yellowish green, often lustrous above, reddish brown to whitish yellow below, stiffly coriaceous. Peduncles uniflorous, slightly flattened, about 0.5 mm wide, 1–4 mm long, densely pubescent, solitary or 2–3 in a row in the axils of leaves; bracteoles ovate to broadly oblong, 0.9–1.5 mm long, 0.7–1 mm wide, 1–2 times as long as wide, coriaceous, densely pubescent without, sparsely pubescent within, clasping the hypanthium; calyx lobes ovate to suborbicular, strongly concave, 1.2–2.6 mm long and wide, usually 0.8–1 times as long as wide, densely to sparsely pubescent without, sparsely pubescent to glabrous within; hypanthium obconic, densely pubescent, ca. 2 mm long; disk 2–2.5 mm across, densely pubescent; style 5–6 mm long, sparsely pubescent; stamens 60–100, 3–6 mm long; anthers 0.4–0.6 mm long when dry; petals more or less orbicular, 2–3 mm in diam., very sparsely pubescent within and without; ovary 2–4-locular; ovules 5–13 per locule. Fruit 4–8 mm in diam., yellow to orange, pubescent; seeds usually destroyed by insects (Fig. 12M).

DISTRIBUTION (Fig. 15A).—A small dense shrub restricted to coastal habitats from central Coquimbo to just north of San Antonio.

PHENOLOGY.—Flowering mainly from August to October; fruits mature in February and March. Insects commonly decimate the seeds so that it is often difficult to find mature ones. There was a relatively good seed crop in 1988 after a very wet winter that may have affected the insect population.

Myrceugenia rufa is easily distinguished from other species by its small thick leaves that have revolute margins, and which show little or no venation.

8.14. **Myrceugenia schulzei** Johow, Estud. Fl. Juan Fernández 96. 1896.

Luma schulzei (Johow) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:526. 1941.

Tree up to 12 m high; hairs yellow to yellow brown, almost entirely symmetrically dibrachiate; twigs densely lanate when young, glabrescent with age, the young twig bark greyish to yellowish white, sometimes tinged with reddish brown, persisting as strips. Leaves elliptic, ovate, obovate, lanceolate, or oblanceolate, 1.5–5(–6) cm long, 0.5–3 cm wide, 1.4–2.8 times as long as wide, densely lanate below when young, densely lanate to glabrous above, glabrescent on both surfaces with age, the smaller, narrower leaves on flower bearing branches; apex acuminate, acute to rounded; base acuminate, cuneate, acute, or obtuse; petiole channeled, 1–4 mm long, 0.5–1.5 mm thick, densely lanate when young, sometimes glabrescent; midvein shallowly impressed proximally, to not at all impressed above, prominent below; lateral veins indistinct or up to about 10 pairs faintly visible; marginal veins about as prominent as laterals or less so; blades

coriaceous, grey green, yellow green, or tinged with reddish brown above, the same or somewhat lighter below. Peduncles uniflorous or bearing a 3 (rarely more)-flowered dichasium, flattened, 0.5–2 cm long, ca. 0.5 mm wide, densely lanate (rarely glabrous), solitary or up to 3 in a row in the axils of leaves; bracteoles ovate to lanceolate, 1–2 mm long, 0.8–1 mm wide, 1.2–2.3 times as long as wide, submembranous, densely to sparsely covered with hairs, rarely glabrous without, glabrous or nearly so within, clasping the hypanthium; calyx lobes ovate-oblong, 1–3 mm long, 1–2.2 mm wide, 0.8–1.5 times as long as wide, sparsely covered with hairs (rarely glabrous) without, sparsely covered with hairs to glabrous within, concave; petals glabrous or nearly so, suborbicular, 2–3.5 mm in diam.; hypanthium obconic, 1.5–2.5 mm long, densely lanate; disk 2–3 mm across, sparsely covered with hairs to glabrous; stamens 90–140, 4–7 mm long; anthers orbicular to oblong, 0.3–0.5 mm long; style 4–6 mm long, glabrous or nearly so; ovary 2–4-locular; ovules 6–12 per locule. Fruit unknown.

DISTRIBUTION (Fig. 15A).—A tree endemic to Masafuera of the Juan Fernández Islands.

PHENOLOGY.—Flowering from January to April; fruiting period unknown.

Myrceugenia schulzei is distinguished by its yellowish brown indumentum of curly symmetrically dibrachiate hairs, and dichasial inflorescence.

GENUS OF UNCERTAIN AFFINITY

9. **Luma** A. Gray, U.S. Expl. Exped., Phan. 535. t. 66. 1854.

Myrceugenella Kausel, Revista Argent. Agron. 9:42. 1942.

Shrubs or small trees up to ca. 10 m high, weakly to strongly glandular, variously puberulent to villous; hairs unicellular, simple. Leaves persistent, subcoriaceous to submembranous, mainly elliptic. Inflorescence uniflorous, or a dichasium of 3 (rarely more) flowers; flowers tetramerous, the calyx lobes ovate-triangular to ovate-orbicular, concave; bracteoles linear, membranous, caducous at or before anthesis; ovary bilocular; ovules ca. 6–14 per locule. Fruit a fleshy, somewhat spongy berry; seeds lenticular, 1–16 per fruit; embryo with the cotyledons suborbicular, thinly planoconvex, slightly fleshy, unfused, the hypocotyl cylindrical, about as long as the cotyledons (Figs. 11B, 17C).

Luma is distinguished from other Chilean Myrtaceae by its membranous testa and unique embryo (Fig. 11B, 17C) with suborbicular, thinly planoconvex cotyledons of about the same length as the hypocotyl. In flower it can be distinguished by tetramerous flowers, bracteoles that are caducous at or before anthesis, and relatively small, elliptic to suborbicular leaves with acute to apiculate apexes.

The name *Myrceugenella* has commonly been used for this genus since it was proposed by Kausel (1942). *Luma* has priority over *Myrceugenella* and the latter name is nomenclaturally superfluous because it is based on the same type species as *Luma* (McVaugh 1956; Landrum 1986).

KEY TO THE SPECIES OF *LUMA*

1. Inflorescence a solitary flower or a dichasium of 3 (rarely more) flowers; leaves usually elliptic or suborbicular, the apex typically abruptly acuminate-apiculate; blades without noticeable glands or with only scattered glands; bark of the trunk greyish to bright orangish brown; habitat often near water but usually in seasonally dry areas ..... 9.1. *L. apiculata*
1. Inflorescence a solitary flower; leaves usually lanceolate, ovate or elliptic, the apex usually acute or only slightly apiculate; blades usually strongly glandular; bark of the trunk greyish brown; habitat usually continually wet, stream beds, marshes, or swamps ..... 9.2. *L. chequen*

9.1. **Luma apiculata** (A. P. de Candolle) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:523. 1941.

Eugenia apiculata A. P. de Candolle, Prodr. 3:276. 1828.
Eugenia gilliesi W. J. Hooker et Arnott, Bot. misc. 3:320. 1833.
Eugenia affinis Gillies ex W. J. Hooker et Arnott, Bot. misc. 3:321. 1833.
Eugenia hookeri Steudel, Nomencl. bot., ed. 2, 603. 1840.
Eugenia apiculata var. *Arnyan* J. D. Hooker, Fl. Antarct. 277. 1846.
Eugenia barneoudii Berg, Linnaea 27:263. 1856.
Eugenia spectabilis R. A. Philippi, Linnaea 28:639. 1857.
Eugenia modesta R. A. Philippi, Bot. Zeitung (Berlin) 15:400. 1857; Linnaea 28:688. 1858.

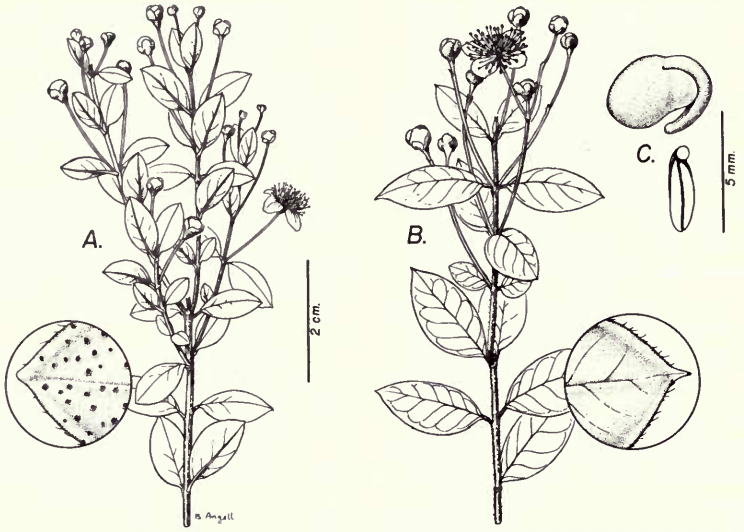


FIGURE 17. *Luma. Luma chequen* (*Rusby 583* at NY): A, young branch with solitary flower inflorescences and an insert showing the upper leaf surface. *Luma apiculata*: B, young branch with solitary flower and dichasial inflorescences from which some flowers have fallen; and an insert showing the upper leaf surface (*Landrum 4372* at NY). C, embryo (*Landrum 4425* at NY). Drawn by Bobbi Angell.

Eugenia proba Berg, Linnaea 29:225. 1858.
Eugenia mucronata R. A. Philippi, Anales Univ. Chile 27: 327. 1865; Anales Univ. Chile 84:756. 1893.
Eugenia palenae Philippi, Anales Univ. Chile 84:756. 1893.
Eugenia cuspidata Philippi, Anales Univ. Chile 84:755. 1893.
Eugenia ebracteata F. Philippi, Anales Univ. Chile 84:758. 1893.
Myrceugenia apiculata (A. P. de Candolle) Niedenzu *in* Engler et Prantl, Nat. Pflanzenfam. 3(7):74. 1893.
Myrtus chequenilla O. Kuntze, Revis. gen. pl. 3(2):90. 1898.
Luma gilliesi (W. J. Hooker et Arnott) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:523. 1941.
Luma spectabilis (R. A. Philippi) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:523. 1941.
Luma hookeri (Steudel) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:526. 1941.
Myrceugenella apiculata (A. P. de Candolle) Kausel, Revista Argent. Agron. 9:47. 1942.
Myrceugenella apiculata var. *genuina* Kausel, Revista Argent. Agron. 9:48. 1942.
Myrceugenella apiculata var. *spectabilis* (R. A. Philippi) Kausel, Revista Argent. Agron. 9:49. 1942.
Myrceugenella apiculata var. *australis* Kausel, Revista Argent. Agron. 9:49. 1942.
Myrceugenella grandjotii Kausel, Revista Argent. Agron. 9:50. 1942.
Myrceugenella apiculata var. *nahuelhuapensis* Kausel, Revista Argent. Agron. 9:236. 1942.

Shrub or small tree up to ca. 10 m high, the trunk smooth, appearing somewhat twisted, the bark greyish to bright orangish brown; hairs whitish, 0.1–1 mm long, straight or curled; young twigs light reddish brown, densely to sparsely puberulent to villous, becoming glabrescent with age. Leaves elliptic to suborbicular, less often ovate or lanceolate, 1–4.5 cm long, 0.5–3.5 cm wide, glabrous or villous to puberulent along the midvein and margins below; apex apiculate or abruptly acuminate, terminating in an apiculum ca. 1 mm long; base acute to rounded; petiole 1–2 mm long, 0.5–1 mm wide, puberulent to villous; midvein flat or slightly impressed proximally above, prominent below; lateral veins indistinct or up to ca. 8 pairs faintly visible; marginal veins equalling laterals in prominence; blades subcoriaceous, somewhat fleshy when fresh, drying reddish brown, greyish brown, or dark olive green, somewhat darker above than below, not noticeably glandular or with a few scattered glands, the lower surface usually somewhat striate, the margins usually revolute. Peduncles uniflorous or bearing a dichasium of 3 (rarely more) flowers, 5–30 cm long, ca. 0.5 mm wide, villous, puberulent, or glabrous; bracteoles membranous, deciduous before anthesis, narrowly lanceolate-triangular, ca. 1–1.5 mm long, sparsely puberulent; calyx lobes triangular-ovate to suborbicular, 2–3(–4) mm long and wide, about as wide as long, ciliate, otherwise glabrous or nearly so; petals suborbicular, ca. 3–5 mm long, ciliate, otherwise glabrous; hypanthium glabrous or nearly so, ca. 2–3 mm long, the sides concave;

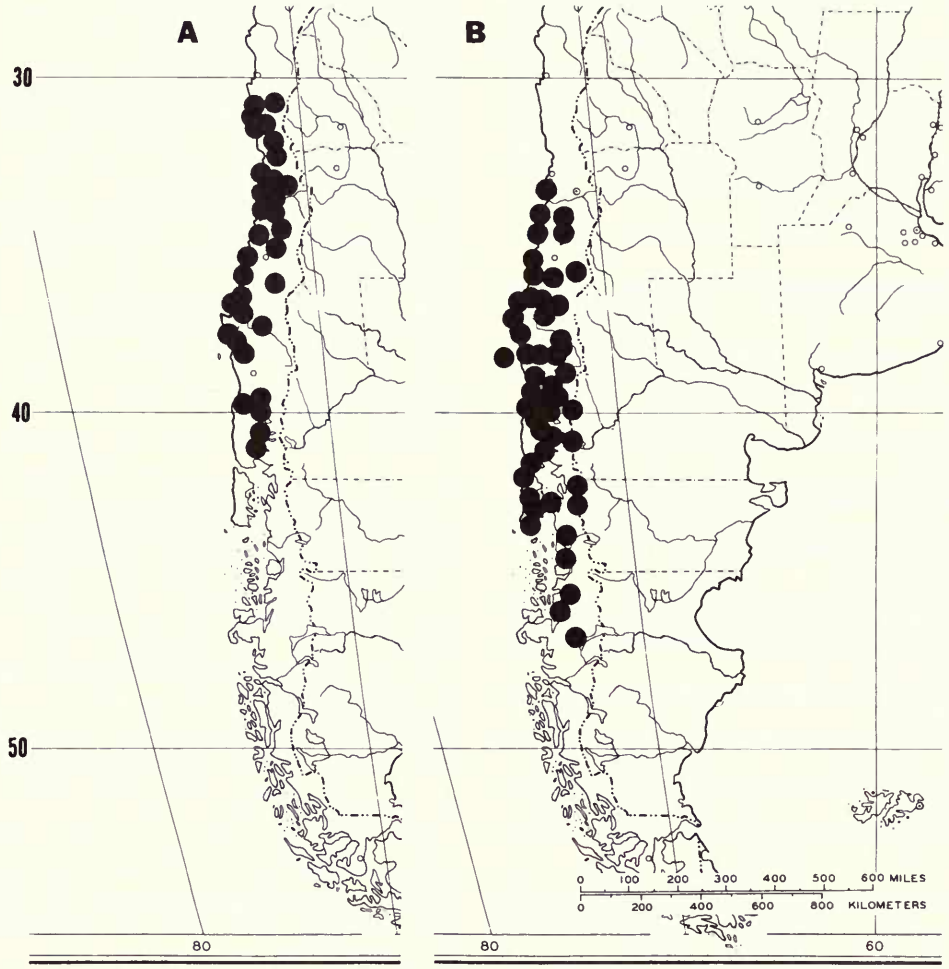


FIGURE 18. Distribution of *Luma chequen* (A) and *L. apiculata* (B).

disk ca. 3 mm across, sometimes becoming a raised cone at the base of the style shortly after the petals and stamens fall; stamens 170–300, ca. 5–7 mm long; anthers ca. 0.4 mm long; style 6–7 mm long, normally glabrous; ovary 2-locular; ovules 6–14 per locule. Fruit subglobose, up to ca. 1 cm in diam., dark purple; seeds 1–16 per fruit, 3–6 mm long (Fig. 17B, C).

DISTRIBUTION (Fig. 18B).—A shrub or small tree of matorral and forests from Valparaíso to Aisén in Chile and in the forested regions of Río Negro, Neuquén, and Chubut in Argentina. Usually growing in localities with abundant humidity during at least part of the year, but not in soils that are continuously wet.

PHENOLOGY.—Flowering from December to May but most abundantly from January to March. Fruiting mainly in March and April.

LOCAL NAMES AND USES.—Arrayán, palo colorado, temu, temo, collimamol, collimamul (Muñoz 1966). Used for handles of tools and domestic utensils (Rodríguez et al. 1983). I have seen the attractive orangish brown trunks of small trees used in woven fences in Chiloé. This species is cultivated in California and England.

Luma apiculata is perhaps the most common and widespread species of Myrtaceae in temperate western South America. In most regions the bark of the trunk is various shades of bright orangish brown, with white spots where bark has recently exfoliated. It is most likely to be con-

fused with *L. chequen* (for distinguishing characters see key), continental species of *Myrceugenia,* which have persistent bracteoles (not deciduous as they are in *Luma*), or *Blepharocalyx cruckshanksii,* which normally has leaves with emarginate apexes (not apiculate or abruptly acuminate as in *L. apiculata*).

9.2. **Luma chequen** (Molina) A. Gray, U.S. Expl. Exped., Phan. 536. 1854. 'Cheken.'

Myrtus folio subrotundo vulgo Cheken, Feuillée, J. obs. 1725.
Eugenia chequen Molina, Sag. stor. nat. Chili, ed. 2, 148, 289. 1810.
Myrtus chequen (Molina) Sprengel, Syst. veg. 2:485. 1825. 'Cheken.'
Eugenia gayana Barnéoud, *in* Gay, Fl. Chil. 2:390. 1847.
Myrtus uliginosa Miquel, Linnaea 25:652. 1852.
Myrtus uliginosa forma *major* Miquel, Linnaea 25:652. 1852.
Myrtus gayana (Barnéoud) Berg, Linnaea 27:399. 1856.
Eugenia bella Philippi, Linnaea 28:641. 1858.
Eugenia pulchra Berg, Linnaea 29:224. 1858.
Eugenia myrtomimeta Diels, Bot. Jahrb. Syst. 37:598. 1906.
Luma gayana (Barneoud) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15:523. 1941.
Myrceugenella chequen (Molina) Kausel, Revista Argent. Agron. 9:43. 1942.
Myrceugenella gayana (Barnéoud) Kausel, Revista Argent. Agron. 9:46. 1942.
Myrceugenella langerfeldtii Kausel, Revista Argent. Agron. 11: 324. 1944.
Myrceugenella chequen var. *myrtomimeta* (Diels) Kausel, Lilloa 33:104. 1972. "1971."

Shrub or small tree up to ca. 9 m high, the bark greyish brown; hairs whitish, 0.1–0.5 mm long; young twigs glabrous to densely puberulent, usually densely glandular, yellowish brown or light reddish brown, becoming brownish grey with age. Leaves elliptic, ovate, or lanceolate, rarely suborbicular, 0.5–2.5(–4) cm long, 0.4–1.5(–1.8) cm wide, 1.3–3 times as long as wide, glabrous or puberulent along the midvein and margins below; apex acute or scarcely acuminate, with or without an apiculum ca. 0.5 mm long; base acute to rounded; petiole 0.5–2 mm long, 0.5–1 mm wide, densely puberulent to glabrous; midvein flat or only slightly impressed above, prominent below; lateral veins indistinct or a few pairs faintly visible; marginal veins equalling laterals in prominence; blades submembranous to subcoriaceous, drying greyish green, somewhat darker above than below, normally strongly glandular, the margins revolute or not. Peduncle uniflorous, 0.5–2.5 cm long, ca. 0.5 mm wide, glabrous to sparsely puberulent; bracteoles linear, 1–2 mm long, 0.2–0.3 mm wide, puberulent, normally deciduous before anthesis; calyx lobes concave, ovate-orbicular, 1.8–3.2 cm long, 2–3 cm wide, ca. 1–1.5 times as long as wide, ciliate, glandular; petals suborbicular, ca. 4–7 mm long, ciliate or glabrous; hypanthium glabrous to sparsely puberulent, glandular, funnel-shaped, 2–3 mm long, the sides concave; disk ca. 2–3 mm across, raised only slightly in the center after the petals and stamens fall; stamens ca. 90–230, ca. 3–7 mm long; anthers ca. 3–5 mm long; style ca. 7 mm long, normally glabrous; ovary 2-locular; ovules 6–11 per locule. Fruit subglobose, 0.6–1 cm in diam., dark purple; seeds 1–9 per fruit, 3–5 mm long (Fig. 17A).

Distribution (Fig. 18A).—A small tree or shrub in Chile from Coquimbo to Llanquihue. Typically growing in habitats that are continually wet such as stream beds, marshes, and the edges of lakes, often in association with *Juncus.*

Phenology.—Flowering from November to April but mainly from December to March. Fruits mainly maturing from February to April.

Local Names and Uses.—Chequén, arrayán blanco, arrayán (Muñoz 1966). *Luma chequen* is reported to have various medicinal uses (Muñoz et al. 1981) and was exported by Park Davis and Co. in the late 19th century (Rusby 1935).

Luma chequen is most likely to be confused with *L. apiculata* (see key for distinguishing characters) or some continental species of *Myrceugenia,* which all have persistent bracteoles (not deciduous as they are in *Luma*).

In the southern part of its range *Luma chequen* is small-leaved and has traditionally been given a different name (*Eugenia gayana,* or its equivalent in *Myrtus, Luma,* or *Myrceugenella*).

Acknowledgments

I began work on this paper at the California Academy of Sciences and finished it at Arizona State University, but my studies of Chilean Myrtaceae date back to when I was a member of Peace Corps in Chile from 1969 to 1973, working in the Escuela de Ingeniería Forestal of the Universidad de Chile in Santiago. Since then my studies of Myrtaceae have continued at the University of Michigan (as a graduate student), the New York Botanical Garden (as B. A. Krukoff Research Associate), the California Academy of Sciences (as Tilton Fellow), and Arizona State

University (as Herbarium Curator). Colleagues at these institutions have been very helpful. Special thanks go to Rogers McVaugh, my major professor at the University of Michigan, and my wife Sonia, who has helped me in numerous ways in my research. The following persons have kindly aided me with arrangements for accommodations and transportation for field studies: Sr. Claudio Donoso, Dr. Carlos Ramírez, and Dr. Anton Huber, Universidad Austral, Valdivia; Sr. Clodomiro Marticorena, Universidad de Concepción; Sra. Mélica Muñoz, Museo de Historia Natural, Santiago; Sr. Jurgen Rottmann, Corporación Nacional Forestal, Santiago; Sra. Raquel Carrasco de Cubillos, Santiago; Sr. Alejandro Suanes, Concepción; and Sr. Francisco Chávez, Valdivia.

The following institutions allowed me to study their specimens of Chilean Myrtaceae as a visitor or by sending loans: A, ASU, CAS, CONC, CTES, DS, E, E-GL, EIF, F, G, GH, H, HBR, K, LE, LP, M, MBM, MICH, MO, MVM, NY, OS, SGO, SI, UC, US, VALD, and W.

Fieldwork and visits to South American herbaria were made possible through National Science Foundation grants DEB-7621543 and DEB-8111063 and a Research Incentive Award from Arizona State University.

I am very grateful to Dr. Rudolph Schmid, Sr. Clodomiro Marticorena, Sr. Claudio Donoso, and three anonymous reviewers who all offered many helpful suggestions as to how this paper could be improved.

Literature Cited

Dawson, J. W. 1972. Pacific capsular Myrtaceae 8. *Tepualia.* Blumea 22:335–337.

Kausel, E. 1940. Revisión de las Mirtáceas Chilenas [1–4]. Pamphlet published by author. Santiago, Chile.

———. 1942. Contribución al estudio de las Mirtáceas chilenas. Revista Argent. Agron. 9:39–64.

———. 1944. Contribución al estudio de las Mirtáceas chilenas, suplemento. Revista Argent. Agron. 11:320–327.

———. 1948 ("1947"). Notas Mirtológicas. Lilloa 13:125–149.

———. 1949. Notas Mirtológicas (suplemento). Lilloa 17: 51–55.

Landrum, L. R. 1975. Un híbrido entre *Myrceugenia exsucca* y *Myrceugenia lanceolata.* Facultad de Ciencias Forestales, Universidad de Chile. Bol. Téc. No. 30:5–10.

———. 1981. A monograph of the genus *Myrceugenia* (Myrtaceae). Flora Neotrop. Monogr. 29:1–137.

———. 1984. The taxonomic implications of the discovery of calyptrate species of *Myrceugenia* (Myrtaceae). Brittonia 36(2):161–166.

———. 1986. *Campomanesia, Pimenta, Blepharocalyx, Legrandia, Acca, Myrrhinium,* and *Luma.* Flora Neotrop. Monogr. 45:1–179.

———. 1988. Systematics of *Myrteola* (Myrtaceae). Systematic Botany 13(1):120–132.

Landrum, L. R., and F. T. Grifo. 1988. *Myrcianthes* (Myrtaceae) in Chile. Brittonia 40:290–293.

McVaugh, R. 1956. Nomenclatural notes on Myrtaceae and related families. Taxon 5:133–147, 162–167.

Moore, D. M. 1983. Flora of Tierra del Fuego. Missouri Botanical Garden, St. Louis, Missouri.

Muñoz P., C. 1966. Sinopsis de la flora chilena, ed. 2. Santiago.

Muñoz S., M., E. Barrera M., and I. Meza P. 1981. El uso medicinal y alimenticio de plantas nativas y naturalizadas en Chile. Mus. Nac. Hist. Nat. Publicación Ocasional 33:3–89.

Navas, E. 1970. Distribución geográfica de las Mirtáceas Chilenas. Bol. Mus. Nac. Hist. Nat. Chile 29:223–247.

Reiche, C. F. 1897. [Myrtaceae in] Estudios críticos sobre la flora de Chile. Anales Univ. Chile 98:695–727.

Rodríguez, R., O. Matthei, and M. Quezada. 1983. Flora Arborea de Chile. Universidad de Concepción, Chile.

Rusby, H. H. 1935. Jungle memories. Whittlesey House, McGraw-Hill, New York, Pp. 82–98.

Sanders, R. W., T. F. Stuessy, and R. Rodríguez. 1983. Chromosome numbers from the flora of the Juan Fernández Islands. Amer. J. Bot. 70(6):799–810.

Appendix A

A list of specimens studied by the author while preparing this paper is available upon request. It is organized by collector and number and each collection is identified as to taxon. This list has been deposited in the libraries at the following herbaria: ASU, CAS, CONC, CTES, F, GH, H, LIL, LP, MICH, MO, NY, OS, SGO, UC, and US.

CALIFORNIA ACADEMY OF SCIENCES
Golden Gate Park
San Francisco, California 94118

INDEX TO VOLUME 45

(Compiled by Tomio Iwamoto)

New names

Acanthemblemaria **stephensi** 104–110
Antipaluria **caribbeana** 25–26
Antipaluria **marginata** 26
Antipaluria **panamensis** 22–23
Antipaluria **silvestris** 24–25
Chromatoclothoda 26–27
Chromatoclothoda **albicauda** 30
Chromatoclothoda **aurata** 29–30
Chromatoclothoda **elegantula** 27–29
Chromatoclothoda **nana** 31–34
Chromatoclothoda **nigricauda** 30–31
Clothoda **longicauda** 15–17
Coryphaenoides **myersi** 71–72
Coryphaenoides **oreinos** 68–71
Cryptoclothoda 17
Cryptoclothoda **spinula** 18–19
Eucryphycus 93–94
Letholycus 272–273
Letholycus **magellanicus** 275–276
Phocavis 98–99
Phocavis **maritimus** 99
Plesienchelys 268
Schizomus **secoensis** 83–86
Stylobatus **loisetteae** 2–6

New names in **boldface** type

Acanthaceae 111–113, 115
Acanthemblemaria 103–104, 106, 108–110
  balanorum 104, 109
  betinensis 109
  blanorum 108
  castroi 104, 106, 108–109
  chaplini 106, 109
  crockeri 104, 108–109
  exilispinus 104, 106, 108
  greenfieldi 109
  hancocki 104, 109
  hancocki group 110
  hancocki species complex 103
  hancocki species group 109
  macrospilus 104, 109
  maria 109
  medusa 109
  rivasi 109
  stephensi 103–104, 106–110
Acanthoideae 112
Acanthus 111
Achnanthes 130, 141, 152
  brevipes 152, 210
  brevipes var. *intermedia* 152, 210
  conspicua var. *brevistriata* 152, 210
  groenlandica var. *phinneyi* 152, 210
  haukiana 143, 147–150, 153, 210
  haukiana var. *rostrata* 153, 210
  lanceolata 153, 210, 226
  longipes 153, 210
  parvula 153, 212
  wellsiae 153, 210, 212
  yaquinensis 153, 212
Acreugenia 284
Actiniidae 1
Actinocyclus 153
  normanii 153, 192
  normanii f. *subsalsa* 153, 192
  octanarius 153, 194
  sp. 1 153
Actinocyclus?
  sp. 1 194
Actinoptychus 153
  senarius 143, 145, 150, 153, 202
  splendens 154, 202
Adamsia 6
  palliata 1, 5
Aequicercata Group 20, 21
Albatrossia 38, 39
  pectoralis 36, 75
Alvinia
  compacta 260
Amasonia
  integerrima 112, 119
Amomyrtus 277–280, 285–286, 309
  luma 277, 285–287, 290, 309
  meli 285–288
Amphipleura 154
  rutilans 154, 214
Amphora 154
  granulata 154, 230
  ovalis 154
  sp. 1 154, 230
  sublaevis 154, 230
  ventricosa 154, 230
Amyrsia 291
Anamomis 284
Ancylogyne 112
Androcentrum 112, 118
  multiflorum 112, 118, 120, 122
Anhinga 100

Anhingidae 100
Anisembiidae 9
Anomoeoneis 154
sphaerophora f. *costata* 154, 220
Antipaluria 10, 13, 17, 19–20, 25–27
aequicercata 19–23, 25–26
caribbeana 9, 11, 20, 24–26
intermedia 9, 20, 24–25
marginata 9, 20, 26
panamensis 9, 20–23
silvestris 9, 20, 24
urichi 9, 20, 23–25
Apis
mellifera 118
Arachnoidiscus 154
ehrenbergi 154
ehrenbergii 204
Archosticum 128
Aspidogenia 284
coquimbensis 284
Asteromphalus 154
Aulacosira 154
ambigua 154, 178
granulata 154, 178
islandica 154, 180
italica 155, 178
Auricula 155
complexa 155, 234
Austrolycus 273
Aves 97

Bacillaria 155
paxillifer 146, 150, 155, 238
Bacillariophyceae 130
Balanus
sp. 259–260, 263–264
Biddulphia 155
alterans 155
alternas 204
aurita 155, 202
laevis 155, 204
Bignonia
bibracteata 119
Bignoniaceae 112
Bittium
eschrichtii 260, 263–264
Blepharocalyx 277–279, 282, 288–289
cruckshanksii 277, 280, 282–283, 287–289, 305, 316
divaricatus 288
divaricatus var. *obovatus* 288
divaricatus var. *ovalis* 288
divaricatus var. *pauciflorus* 288
eggersii 288
salicifolius 288
subgen. *Temu* 288
Bogoslovia 39, 75
clarki 75
Bothrocara 89
Brachyura
indet. 259–260
Bravaisia 111–113, 115–120
berlandieriana 111, 113, 115–119, 126–128
floribunda 112, 118–119
grandiflora 111–113, 115–119, 124–126, 128–129
integerrima 111, 113, 115–123, 128–129
proxima 112, 124–125
tubiflora 112, 115, 126–128
Brosimum 122
Bursera 122

Caloneis 155
alpestris 155, 220
amphisbaena 155, 220
bacillum 155, 220
ventricosa 155, 220
westii 155, 220
Campylodiscus 155
blypeus 155
clypeus 246
echeneis 155–156, 246
incertus 156, 242
ralfsii 156, 242
Caralliozetus
angelica 107
Cariburus 39
Cerataulus 156
turgidus 156, 204
Chaenopsidae 103
Chaetoceros 156
cinctus 156, 206
lorenzianus 156
mitra 156, 206
radicans 156
sp. 1 156, 206
sp. 2 156
Chaetoceros?
sp. 2 206
Chalinura 39, 76
carapinus 76
fernandezianus 77
simula 76
Chromatoclothoda 9–10, 12–13, 17, 26–27
albicauda 9, 12, 27, 30–31
aurata 9, 27–29
elegantula 9, 26–29, 33
nana 9, 27, 31, 33–34
nigricauda 9, 27, 30, 32
Clinocardium
nuttallii 259–260
Cliona
sp. 259–260
Clothoda 9–13, 17–20, 27
aequicercata 21

intermedia 23–24
longicauda 9, 11–17, 26
nobilis 13–16, 26
urichi 23
urichi intermedia 24
Clothodidae 9–10
Clothodinae 10
Cluacena 291
Cocconeis 130, 141, 156
californica 156, 212
decipiens 156, 212
diminuta 156, 212
fasciolata 157, 214
placentula 157, 212
scutellum 157, 212, 214
sp. 1 157, 212
sp. 2 157, 214
vitrea 143, 150, 157, 212
Cocothrinax 128
Coelenterata 1
Coelorinchus 38–39, 52
canus 38
Conger
punctus 89–90
Conocarpus 128
Coryphaenoides 35–36, 38–40, 42, 45–46, 50, 52–53, 58–59, 64, 66, 68, 71, 75–77
Coryphaenoides (*Chalinura*) 35–36, 38, 59, 71, 75–77
brevibarbis 42
fernandezianus 36, 42, 70
leptolepis 42
liocephalus 42
mediterranea 42
murrayi 42
profundicola 42
striatura 42
Coryphaenoides (*Coryphaenoides*) 35–36, 42, 45–46, 50, 53, 58–59, 62, 64, 68, 71, 73, 75
acrolepis 40
aequatoris 40
alateralis 40
altipinnis 40
anguliceps 35, 40
ariommus 35, 40
asper 40
asprellus 40
boops 35, 40
bucephalus 35, 40
bulbiceps 35, 40
camurus 40
capito 35, 40
carminifer 35, 40
cinereus 40
delsolari 35, 40
dubius 40
filamentosus 40
filifer 40
guentheri 40
hextii 40
hoskynii 40
longicirrhus 42
longifilis 42
macrocephalus 42
macrolophus 42
marginatus 42
marshalli 42
mexicanus 42
microps 42
myersi 36, 42
nasutus 42
oreinos 35, 42
orthogrammus 42
paradoxus 36, 42
paramarshalli 42
rudis 42
rupestris 42
semiscaber 42
serrulatus 42
sibogae 42
subserrulatus 42
thelestomus 42
tydemani 42
woodmasoni 42
zaniophorus 42
Coryphaenoides (*Lionurus*) 35–36, 38–39, 42, 78–79
carapinus 42, 79
filicauda 36, 42
Coryphaenoides (*Nematonurus*) 35, 36, 38, 40, 42
affinis 42
armatus 36, 42, 75
ferrieri 42, 75
lecointei 42, 75
paradoxus 72
yaquinae 42, 75
Coryphaenoides
altipinnis 68
anguliceps 35, 42, 44–45, 47–50, 53, 63, 70
ariommus 35, 42, 44–45, 47–50, 52–53, 58, 63, 70
armatus 35, 40, 61, 76
armatus armatus 40, 75–76
armatus variabilis 40, 76
boops 35–36, 42, 44, 50, 53–57, 63, 66
brevibarbis 77
bucephalus 35, 42, 56–57, 59–61, 68, 70, 72
bulbiceps 35, 42, 56, 59, 68, 70, 74–75
capito 35, 42, 44, 50, 53, 56–57, 62–64, 66, 72
carapinus 79
carminatus 64
carminifer 35, 44, 57, 64–66, 72
delsolari 35, 42, 66–68
fernandezianus 35, 44, 53, 77
filicauda 35, 37, 40, 56, 78–79
filifer 59
latinasutus 35, 45
leptolepis 40, 76–77

liraticeps 45
longicirrhus 59, 61, 75
longifilis 45, 75
macrocephalus 40, 61, 73–74
macrolophus 56
marginatus 55–56
microps 56
murrayi 77
myersi 35–36, 44, 56–57, 64, 66, 71–72
oreinos 35, 40, 44, 58, 68–70, 77
paradoxus 35–36, 40, 61, 68, 70, 72–75
paramarshalli 39
rudis 40, 75
rupestris 38–39
semiscaber 56
serrulatus 38–39, 45
sp. 73
subserrulatus 38–40, 45
thelostomus 61
tydemani 56
variabilis 76
yaquinae 38, 40, 76
zaniophorus 66
Coscinodiscus 157
angstii 177
asteromphalus 158
curvatulus 157, 194
decrescens 157, 186
jonesianus 157, 186
marginatus 157, 188, 246
nitidus 157, 190
obscurus 157, 186, 188
oculus-iridis 157–158, 186
radiatus 158, 186, 188
Cryptoclothoda 10–11, 17, 27
spinula 9, 17–19
Cryptomya
californica 259, 263
Cyclotella 158
comta 158, 190
menegheniana 143, 149, 158, 182
pygmaea 158, 182
stelligera 158, 182
striata 130, 141, 158, 182, 190
striata/stylorum 143, 145, 150, 158
stylorum 158, 182
Cylichnella
culcitella var. *eximia* 259–260, 263
Cymatosira 158
belgica 158, 206
lorenziana 158
Cymbella 159
cistula 159, 232
mexicana 159, 212
mexicana var. *janischii* 159, 232
minuta 159, 230
muellerii var. *ventricosa* 159, 232
prostrata 159, 230
prostrata var. *auerswaldii* 159, 230
sinuata 159, 230
triangulum 159, 230, 232
tumidula 159
Cynomacrurus 39
piriei 39
Cypeastroidea
indet. 260

Denticula 159
subtilis 159, 236
thermalis 159
Dialium 122
Diatoma 159
anceps 159, 206
vulgare var. *breve* 159, 206
Dimeregramma 160
minor 160, 206
Diodora
aspera 260
Diplocystis 23
Diploneis 160, 167
bombus 160, 222
decipiens 143, 160, 222
interrupta 160, 222
oblongella 160, 220
oculata 160
ovalis 160
papula var. *constricta* 160, 222
puella 160
smithii 160, 220
sp. 6 160, 222
Ditylum 160
brightwellii 130, 141, 143, 145, 148, 150, 160–161, 206

Echinophoria (*Liracassis*)
rex 100
Echinophoria
dalli 99
rex 100
Ekemblemaria 109
Embia
(*Olyntha*) *nobilis* 13
florissantensis 13
nobilis 13
uhrichi 23
urichi 23
Embiidae 10
Embiidina 9
Emblemaria 108
diphyodontis 108
Entomoneis 161
alata 161, 230
conspicua 161
paludosa 161, 228
pulchra 161
sp. 1 161, 228

Epithemia 161
adnata var. *porcellus* 161, 236
argus 161, 236
sorex 161, 236
turgida 161, 236
turgida var. *westermanii* 161, 236
Eucalyptus 278
Eucryphycus 89, 93, 95–96
californicus 89–92, 94–95
Eugenia
affinis 313
apiculata 313
apiculata var. *Arnyan* 313
barneoudii 313
buxifolia 300
chequen 316
chrysocarpa 300
colchaguensis 301
concinna 289
corralensis 303
correaefolia 301
cruckshanksii 288
cumingii 310
cuspidata 314
darwinii 285
distoma 311
divaricatum 288
divaricatum [var.] α *obovata* 288
divaricatum [var.] β *ovalis* 288
divaricatum [var.] γ *pauciflora* 288
dombeyana 306
ebracteata 314
exsucca 303
exsucca [var.] β *patagua* 303
fernandeziana 305
ferruginea 312
gayana 316
gilliesi 313
gudilla 306
hookeri 313
humifusa 292
leptospermoides 307
leptospermoides [var.] α *microphylla* 307
leptospermoides [var.] β *latifolia* 307
leptospermoides [var.] γ *longifolia* 307
lumilla 305
maritima 301
modesta 313
mucronata 314
multiflora 303
myrtomimeta 316
obtusa 308
ovata 308
palenae 314
parvifolia 310
patagonica 300
petiolata 300
philippi 300
pinifolia 311
pitra 303
planipes 311
planipes [var.] α *genuina* 311
planipes [var.] β *grandiflora* 311
polyantha 308
proba 314
pulchra 316
raran 308
rufa 312
selkirkii 297
spectabilis 313
stenophylla 306
stenophylla [var.] α *angustifolia*
stenophylla [var.] β *latifolia* 306
thalassaia 301
thymifolia 307
trichocarpa 310
ugni 294
Eugenia?
exsucca [var.] δ *apiculata* 303
exsucca [var.] γ *temu* 303
temu 303
Eugeniinae 279, 284
Eunotia 161
arcus 161, 210
arcus var. *bidens* 161, 210
eruca 161, 210
monodon 161, 210
tridon 162, 210
Eunotogramma 162
marina 206
marinum 162
Euodia 177
barbadensis 177

Ficus 122
Fissurella?
sp. 260
Fragilaria 130, 141, 143, 162
brevistriata 162, 208
capucina 162, 208
capucina var. *vaucheriae* 162, 208
construens 145, 150, 162, 208
construens var. *binodis* 162, 208
construens var. *pumila* 162
construens var. *pumilla* 208
construens var. *venter* 162, 208
crotonensis 162, 208
lapponica 162, 208
leptostauron 162, 208
tabulata 162, 208
ulna 163, 208
virescens var. *elliptica* 163, 208
Frustulia 163
asymmetrica 163, 214
interposita 163, 214

Gadiformes 35
Gomphoneis 163
eriense 163
herculeana 163
Gomphonema 163
affine 163, 234
angustatum var. *sarcophagus* 163, 234
apicatum 163
eriense 234
gracile 163, 234
grovei 163, 234
herculeana 234
parvulum 163, 234
rhombicum 163, 234
septum 163, 234
ventricosum 164, 234
Grammatophora 164
marina 164, 206
Granulina
margaritula 260, 263
Guazuma 122
Gymnacanthus 112
Gymnelopsis 89
Gyrosigma 164
acuminatum 164, 216
attenuatum 164
balticum 164, 216
exile 164, 214, 216
eximium 164, 214
fasciola 143, 146, 150, 164, 216

Halictus (*Seladonia*)
tripartitus 118
Hantzschia 164
amphioxys 164, 238
Heliocarpus 122
Hemidiscus 177
Hemimacrurus 39
Hinnites
giganteus 260
Hyalodiscus 164
scoticus 164, 200
Hydrosera 164
triquetra 164, 204
Hymenocephalus 39
Hyomacrurus 38–39

Inga 122
Isadamsia 5–6
Isthmia 154, 164
nervosa 154, 164–165, 204

Laguncularia 128
Legrandia 277–279, 289
concinna 277, 279–280, 289–291
Lepidorhynchus 38–39
denticulatus 39
Leptospermeae 278, 281
Leptospermoideae 278
Letholycus 267–268, 272
magellanicus 267, 269, 275
microphthalmus 269, 271–273
Lionurus 39, 76
carapinus euabyssalis 79
filicauda 77
latinasutus 45
Liracassis
apta 100
rex 100
Lithembia 13
Littorina
scutulata 260
Lonchocarpus 122
Louteridieae 113
Louteridium 111, 113
Luma 277–278, 280, 298, 313–314, 316
apiculata 278, 287, 289, 309, 313–316
baeckeoides 310
chequen 278, 313–315
chrysocarpa 300
corralensis 304
correaefolia 301
cruckshanksii 288
cumingii 310
dombeyana 307
exsucca 303
fernandeziana 305
ferruginea 312
gayana 316
gilliesi 314
hookeri 314
nannophylla 310
obtusa 308
ovata 310
philippi 300
pitra 304
rufa 312
schulzei 312
spectabilis 314
stenophylla 306
Luma?
temu 303
Lycenchelys 89, 95
Lycodes 272
macrops 268
Lycodonus 95

Macoma
nasuta 255, 259–260, 263–264
Macrostegia 112
Macrouridae 35, 45
Macrourus 38–39
boops 39
bulbiceps 59
capito 39

carminifer 39
paradoxus 72
Macrurus (*Chalinurus*)
fernandezianus 77
Macrurus (*Lionurus*)
filicauda 77
Macrurus (*Nematonurus*) 75
armatus 75
Macrurus
acrolepis 39
anguliceps 35, 45
armatus 75
boops 53, 62
bucephalus 57, 68
capito 62, 64
carminifer 64
latinasutus 35, 45–46, 49
leucophaeus 35, 62, 64
liraticeps 35, 45–46, 49
longifilis 39
semiscaber 57
vagrans 62, 64
zaniophorus 39
Malacocephalini 39
Marginata Group 20, 26
Marlieriopsis 288
Mastogloia 165
exigua 165, 214
Maynea 89, 91, 93, 268, 273
californica 89–90, 94
microphthalma 267, 273
microphthalmus 268, 273
patagonica 89, 91
puncta 89–92, 95
Mearnsia 284
Melanostigma
microphthalmus 89, 267, 272–273
Meli 277
Melosira 165
arenaria 165, 180
moniliformis 143, 148, 165, 178
nummuloides 165, 178
numuloides 143
Merceugenella 314
apiculata 314
apiculata var. *australis* 314
apiculata var. *genuina* 314
apiculata var. *nahuelhuapensis* 314
apiculata var. *spectabilis* 314
chequen 316
chequen var. *myrtomimeta* 316
gayana 316
grandjotii 314
langerfeldtii 316
Meridion 165
circulare var. *constrictum* 165, 208
Metrosiderinae 283
Metrosideros
stipularis 281
Mopalia
sp. 259–260, 263–264
Myrceugenia 277–279, 298, 302, 309, 313, 316
apiculata 314
buxifolia 300
camphorata 303
chilensis 308
chrysocarpa 277, 299–302, 304, 312
colchaguensis 277, 299, 301–302, 304
correifolia 277, 299–304
distoma 311
exsucca 277, 289, 299, 303, 305–306
fernandeziana 277, 280, 298, 302, 305–306
ferruginea 312
johowi 301
lanceolata 277, 299, 302, 304–307
lechleriana 303
leptospermoides 277, 299, 302, 306–308
luma 305
malvillana 301
maritima 301
montana 310
multiflora 303
nannophylla 310
obtusa 277, 280, 298–299, 302, 308–309
obtusa [var.] α *raran* 308
obtusa [var.] β *berteroana* 308
obtusa [var.] γ *polyantha* 308
ovata 277, 298, 300, 302, 308–309
ovata var. *nannophylla* 277, 302, 305, 309–311
ovata var. *ovata* 277, 302, 309, 311
parvifolia 278, 299, 302, 309–310
pinifolia 278, 299, 302, 309–311
planipes 278, 300–302, 304, 311–312
rufa 278, 299, 302, 306, 312
schulzei 278, 299, 306, 312–313
stenophylla 306
stenophylla var. *pinifolia* 311
thalassaia 301
valientei 310
Myrcia
lechleriana 285
planipes 311
subgen. *Myrceugenia* 298
Myrcianthes 277–279, 282, 284–285
coquimbensis 277, 280, 282–285
Myrciinae 279, 298
Myrtaceae 277–278, 285, 288–291, 293, 298, 301, 303, 313, 315–316
Myrtastrum 292
Myrteae 278, 284
Myrteola 277–280, 291–292
barneoudii 292
barneoudii var. *humifusa* 292
bullata 292
bullata [var.] α *tetramera* 292

bullata [var.] *β pentamera* 292
humifusa 292
leucomyrtillus 292
nummularia 277, 279–280, 283, 291–293
nummularia var. *repens* 292
repens 292
Myrtinae 279, 285
Myrtoideae 278
Myrtus 285
berteroi 297
candollei 294
chequen 316
chequenilla 314
coquimbensis 284
darwinii 285
fernandeziana 305
folio subrotundo vulgo Cheken 316
gayana 316
gudilla 306
krausei 294
lanceolata 306
leucomyrtillus 292
luma 285
meli 287
multiflora 285
nummularia 292
nummularia var. *β major* 292
raran 308
repens 292
rufa 312
stipularis 281
ugni 294
uliginosa 316
uliginosa forma *major* 316
valdiviana 285
Mysella
tumida 259–260
Mytilus
edulis 259–260

Nassarius
mendicus 260
Navicula 130, 141, 165
abunda 165, 222
auriculata 165, 226
aurora 165, 222
brasiliensis 166
circumtexta 165, 222
cryptocephala 165, 222
cuspidata 165, 222
digito-radiata 166, 222
distans 166, 222
elegans 166
elginensis 166, 224
expansa 166, 226
granulata 166, 224
gregaria 166, 224
humii 166
hummii 224
lanceolata 166
marina 166, 167
mutica 166, 224
peregrina 166, 224, 226
pseudolanceolata 150, 166–167, 226
punctulata 166–167, 224
pusilla 167, 224
pusilla var. 1 167, 224
pygmeae 167, 224, 226
reichardtii 167
reichardtii var. *tschuktschorum* 167, 226
salinarum 167, 224
scopulorum 167, 226
secreta var. *apiculata* 167, 226
spicula 167, 226
subforcipata 167, 226
tripunctata 143, 146, 150, 167, 226
trivialis 166
Nematonurus 39, 75
armatus 75
bulbiceps 59
macrocephalus 73
sp. aff. *altipinnis* 66
Neomyrtus 292
Nitzschia 130, 141, 168, 169
acuminata 130, 141, 143, 146, 148, 150, 168, 238
angularis 168, 242
circumsuta 168, 238
closterium 168, 242
dissipata 168, 240
fasciculata 168, 242
frustulum 168, 242
gandersheimiensis 168, 242
granulata 155, 168, 240
granulata var. 1 168, 240
hummii 168, 242
levidensis 169, 238
longa 169, 242
navicularis 168, 169, 240
obtusa var. *scalpeliformis* 169, 242
panduriformis 169, 240
plana 169, 240
pseudohybrida 169, 240
punctata 169, 238
punctata var. *coarcta* 169, 240
pusilla 143, 146, 148, 169, 240
sigma 169, 242
sigmaformis 143, 147, 149–150, 169, 242
sp. 1 170, 240
tryblionella 169, 238
tryblionella var. *victorae* 169
vitrea 170, 242
Nothofagus
antarctica 310
dombeyi 300
Nothomyrcia 298
fernandeziana 305

Nutricola 265
sp. 259–260

Ocotea 122
Odontomacrurus 39
murrayi 39
Odostomia
nota 255, 259–260, 263–264
Oidiphorus 89, 95
Oligembia 34
Oligotoma 34
saundersii 32
Olyntha
brasiliensis 13
nobilis 13
urichi 23
Onychacanthus 118
arboreus 112, 120
berlandierianus 112, 126, 128
cumingii 112, 118, 120
speciosus 112, 120
Opephora 170
pacifica 170, 208
swartzii 170, 208
Ophiomorpha 261
Ophthalmolycus 268, 272–273
macrops 268
microphthalmus 273
stehmanni 267–268
Opthalmancanthus 112
Orbignya 122
Ostrea 259, 261
lurida 255, 259–260, 262–264

Pachycara 89
Pagurus
prideauxi 5
Paracalliactis 1, 6
Paralia 170
sulcata 130, 141, 143, 145, 148–150, 170, 180
sulcata var. *coronata* 170
Parapagurus 1, 6
dofleini 6
trispinosus 6
Pelecaniformes 97–98, 100–101
Perciformes 267
Perumyia
embiaphaga 17
Phalacrocoracidae 98
Phocavis 98–99
maritimus 97, 99–101
Phucocoetes 95
Pinnularia 170
abaujensis var. *rostrata* 170, 228
acuminata 170, 228
borealis 170, 226, 228
borealis var. *brevicostata* 170, 228
gibba 170, 228
microstauron var. *biundulata* 170, 228
subcapitata var. *paurcistriata* 170, 228
Pisces 103
Pithecellobium 122
Plagiogramma 171
interruptum 171
stauropharum 171
Plagiotropis 171
vitrea 171, 230
Plesienchelys 267–268, 272
stehmanni 268–272
Pleurosigma 171
angulatum 171, 216, 218
australe 171, 218
diverse-striatum 171, 216
formosum 171–172, 218
normanii 171, 216
sp. 1 171, 216
sp. 2 172, 216
strigosum 171–172, 218
Plotopteridae 97–98, 100–101
Plotopterinae 98
Plotopterum 97–98
joaquinensis 97, 100–101
Pogonolycus 95
Polydora
sp. 255, 259–260, 263
Protothaca 263
staminea 255, 259–260, 263–264
Pseudocaryophyllus
darwinii 285
meli 287
sect. *Amomyrtus* 285
Pseudoeunotia 172
doliolus 172, 238
Pyramidellidae 266

Reichea 284–285
coquimbensis 284
Rhabdonema 172
arcuatum 172, 208
Rhaphoneis 172
amphiceros 172, 208
margaritalimbata 172, 208
surirella 172, 208
Rhizophora 128
Rhizosolenia 172
sp. 1 172, 204
Rhoicosphenia 172
curvata 172, 214
Rhopalodia 172
gibba 172, 236
gibberula 172–173, 236
musculus 173
operculata 172–173, 236
Ruellia 111–113
arborescens 120

Ruellieae 112–113
Ruellioideae 112–113

Sanchezia 112–113
Saxidomus 259–261, 263
gigantea 255, 259–260, 263–264
Schizomida 83, 87
Schizomidae 83
Schizomus 83
belkini 83, 86–87
briggsi 83
briggsi group 86
secoensis 83–85
shoshonensis 86
Sclerocalyx 112
Sclerogibbidae 17
Scoliopleura 173
tumida 173, 228
Scoliotropis 173
latestriata 173, 228
Skeletonema 173
costatum 173
Spathipora
sp. 260
Sphagnum 292
Spondias 122
Stauroneis 173
acuta 173, 220
amphioxys 173, 222
obtusa 173, 218
smithii var. *incisa* 173, 218
Steirosanchezia 112
Stephanodiscus 173
astrea 173–174, 184
carconensis 174, 184
lucens 174
niagarae 174, 184
rotula 173–174
Stephanogonia 174
sp. 1 174
Stephanopyxis 174
sp. 1 174
turris 174
Stephanopyxis?
sp. 188
Stylobates 1, 4–6
aeneus 4–6
cancrisocia 4–6
loisetteae 1–6
Suessenguthia 112–113
Sulae 98
Surirella 174
crumena 174, 244
fastuosa 174, 244
gemma 174, 244
ovalis 175
ovalis var. *crumena* 174
ovalis var. *maxima* 175
ovalis var. *pyriformis* 175
ovata 174, 244
peisonis 174–175, 244
pyriformis 175
recedens 175
salina 175
striatula 175, 244
torquata 175, 244
Synedra
fasciculata 162

Tabellaria 175
fenestra 175, 208
Teleostei 267
Temu 288
cruckshanksii 288
divaricatum 288
Tepualia 277–279, 281–283
patagonica 281
philippiana 281
stipularis 277–278, 280–283
stipularis var. *patagonica* 281
stipularis var. *philippiana* 281
Terpsinoe 175
americana 175, 204
Thalassionema 175
nitzschioides 153, 175, 208
Thalassiosira 134, 175, 177
angulata 176
cf. *T. pacifica* 176, 198
decipiens 130, 141, 143, 145, 148–151, 175, 200
decipiens var. 1 175–176, 200
eccentrica 176, 196, 198
hendeyi 176, 196
incerta 176
lacustris 176, 188, 190
lacustris var. *hyperborea* 176
lacustris var. *septentrionalis* 176
nodulolineata 176, 196
pacifica 177
punctigera 177, 194
sp. 1 177, 194
visurgis 176
Tonsala 98
hildegardae 97, 100–101
Trachyneis 177
aspera 177, 234
Trachysphenia 177
acuminata 177, 208
Tresus 261, 263
sp. 255, 259, 263–264
Triceratium 177
dubium 177, 204
Trichanthera 111–113, 117
gigantea 111
Trichanthereae 111–113, 115, 117
Trichosanchezia 112–113

Tricolia?
sp. 260
Trithyreus
belkini 86
Tropidoneis 171
vitrea 171
Turbonilla
raymondi 259–260, 263–264

Ugni 277–280, 293–295
berteroi 297
candollei 277, 294–296
candollei forma *litoralis* 294
candollei forma *monticola* 294
molinae 277, 294, 296–298
myrtus 294
philipii 294
poeppigii 294
selkirkii 277, 294–298
ugni 294
Urichi Group 20, 23

Verbenaceae 112

Whitefieldia 112

Zoarcidae 89, 267
Zosteraceae
indet. 260–261